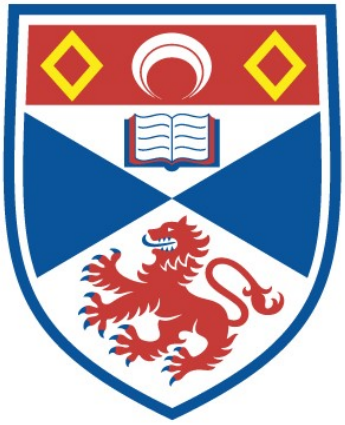
BIODIVERSITY IN THE ANTHROPOCENE: QUANTIFYING ASSEMBLAGE LEVEL CHANGE

Faith Ann Jones

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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Biodiversity in the Anthropocene: Quantifying Assemblage Level Change

Faith Ann Jones

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Abstract

Humans are altering ecosystems at alarming rates, but we do not fully know how anthropogenic pressures are affecting local biodiversity. This knowledge gap poses problems for understanding ecological systems and for undertaking effective conservation initiatives. The aim of this thesis was to increase our understanding of local scale biodiversity change by focusing on assemblages, which are groups of species from the same taxonomic group that live in the same place. I focused on assemblage size, structure and species composition, with the end-goal of making informed suggestions on how to monitor change effectively. First, I asked whether sampling approach was highly influential when estimating species richness and composition of Trinidadian freshwater fish assemblages. I compared assemblage composition of two very different data collections: a systematic survey endeavour and the historical museum records of The University of West Indies. Both datasets provided comparable estimates of species richness, and they both contained mostly the same species. Where they did differ in species lists, they did so among the locally uncommon or specialist species. Next, I asked how closely changes in assemblage size measured in the currencies of numerical abundance and biomass relate. My analysis showed that neither assemblage size quantified in terms of numerical abundance, nor in terms of biomass, is systematically changing across systems, but that change in one currency usually predicted change in the other currency. Thirdly, I asked whether there is evidence for other directional changes across assemblages. There was no evidence of changes in the dominance structure or dominant species body size. There was, however, evidence from increasing numbers of rare species entering assemblages and driving up local species richness, as well as a suggestion of increased turnover among dominant species. Local assemblages therefore are displaying measurable change, but not all metrics capture these changes.

Acknowledgements

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Finally, a big thanks to my husband Peter. You are always there for me. Thank you.

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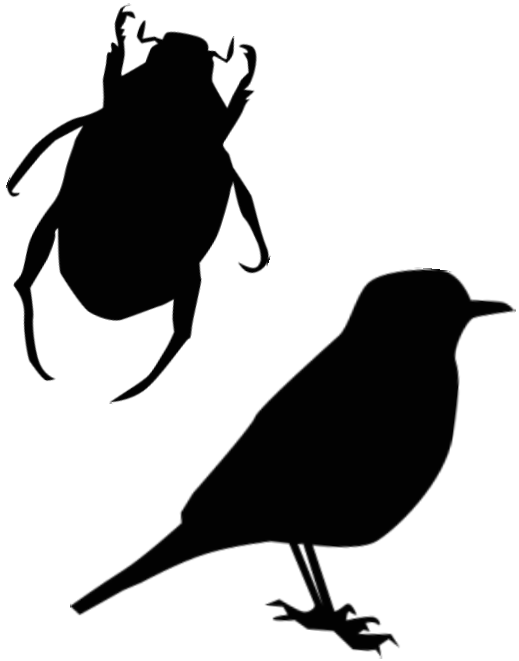
Chapter 1

Introduction



Humans are putting increasing pressure on the ecosystems of our planet, with potentially dire consequences (Ripple *et al*., 2017). The effects of these pressures on biodiversity is currently unclear, but biodiversity change has been the focus of many recent studies (e.g. Barnosky *et al*. 2011; Pereira *et al*. 2012; Dornelas *et al*. 2014). There is much conflicting research on the extent and severity of biodiversity change (e.g Dirzo & Raven 2003; Vellend *et al*. 2013; Dornelas *et al*. 2014; Gonzalez *et al*. 2016; Willis & Bachman 2016). Understanding biodiversity change is important because it can affect ecosystem functioning (Cardinale *et al*. 2011; Hooper *et al*. 2012; Naeem *et al*. 2012), and is consequently predicted to impact human welfare and economy (Perrings *et al*. 1992; Chapin *et al*. 2000; Pinto *et al*. 2014). Knowing how ecosystems react to change is also vital for effective conservation action (Mace *et al*., 2010), and requires an in-depth understanding of the dynamic properties, drivers and mechanisms within ecosystems.

The key questions my thesis will address all relate to local-scale biodiversity change. Before addressing these questions directly, I will provide an overview of the relevant literature. Firstly, I will define the ecological units relevant to assessing biodiversity change, including how an ecosystem's capacity to support life can be defined. Secondly, I will discuss the various ways of quantifying and measuring change. Thirdly, I will provide an overview of different theories and mechanisms relating to biodiversity maintenance and change. Finally, I will lay out the exact questions I will be answering in this thesis.

1.1 Defining ecological units

To understand biodiversity change, one must first have a clear concept of what biodiversity actually means. The term biodiversity, or "biological diversity" in its full form, is extremely broad. The definition provided by the Convention on Biodiversity (CBD) is:

"*variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*" (CBD, 2010).

This definition is far too wide and all-encompassing to be tackled in a single analysis. To aid with understanding biodiversity, ecologists have therefore defined a suite of different ecological units. The term ecosystem was proposed by Tansley (1935) as the basic unit of ecology. His reasoning for this was that biotic and abiotic factors should be considered together because they are fundamentally linked. Ecological data, though, rarely contains

sufficient breadth to allow for the analysis of a full ecosystem. A variety of units with a narrower scope has therefore been proposed for further sub-setting ecosystems.

The term “community” is popular name for the unit of study among ecologists. It is generally used to describe some form of locally grouped species, and has a long history of use in the field of ecology. The first example in the literature of the term “community” was in a study by Möbius (1883) where he describes an oyster bed as a “community of living beings”. What exactly a “community” is, however, has been causing confusion in the literature for almost as long as the term as been in use.

In his discussion on views on the concept of a biological community, Phillips (1931) remarked on how the term community can refer to just plants (with animals as factors), to just animals (with plants as part of the habitat) or plants and animals together. Phillips (1931) concluded that a biotic community should be considered to contain plants, animals, and fungi that all have integrated responses, reactions and co-actions. A spatial element to this definition was added a little later by Shelford (1932), where he describe a community as an aggregation of species of both plants and animals within a particular area. Under this definition of community, the spatial extent of a community could range from 0.5 metres to 1,000,000 square kilometres. Using this definition, ultimately all living things Earth could be considered a single, extremely large, community (Taylor, 1935).

More recently, the exact definition of a community was once again re-examined to try and clarify ecological terminology. Fauth *et al*. (1996) noted that the term “community” was used in the literature to describe groups of species with varying levels of interactions and taxonomic similarity (**Table 1**). This variety causes difficulty when comparing between studies. To address this issue, Fauth *et al*. (1996) proposed a framework of definitions to account for the variety within the concept of a “community” (**Figure 1).** They retain the term community, but distance it from taxonomic and functional species characteristics. Within their framework, a community is a “collection of species occurring in the same place as the same time”, not restricted by phylogeny or resource use. The boundaries of a community could have some biological or environmental reasoning, but they could also be purely arbitrary. A new term, “assemblage”, was introduced to refer to a specific taxonomic group within communities. The term “guild” was also assigned the meaning of a group of species within a community that share a similar resource. In the field of ecology, it is rare to be able to collect data on an entire community, so defining clear subdivisions within communities is useful for interpreting

results. It is this definition of community, and the sub-unit assemblage, that I will use for the duration of this thesis. Because of the challenges of attaining community-wide data, assemblage data is far more prevalent. Consequently, I will focus on change within assemblages rather than communities in my thesis.

Table 1. The definitions of "community" used in several ecology textbooks quoted by Fauth *et al*. (1996). All definitions are direct quotes from the glossaries.

Set Boundaries	Definition	Source
Space, time	The species that occur together in space and time	Begon *et al*. 1990
Space, time, interactions	An association of interacting populations, usually defined by the nature of their interaction or the place in which they live	Ricklefs 1990
	A group of organisms that live alongside one another, and in which the different species interact with one another	(Tudge, 1991)
Space, time, interactions, phylogeny	A group of interacting plants and animals inhabiting a given area	(Smith, 1992)
	An assemblage of interacting plants and animals on a shared site	(Freedman, 1989)
	A group of populations of plants and animals in a given place; an ecological unit used in a broad sense to include groups of various sizes and degrees of integration	(Krebs, 1985)

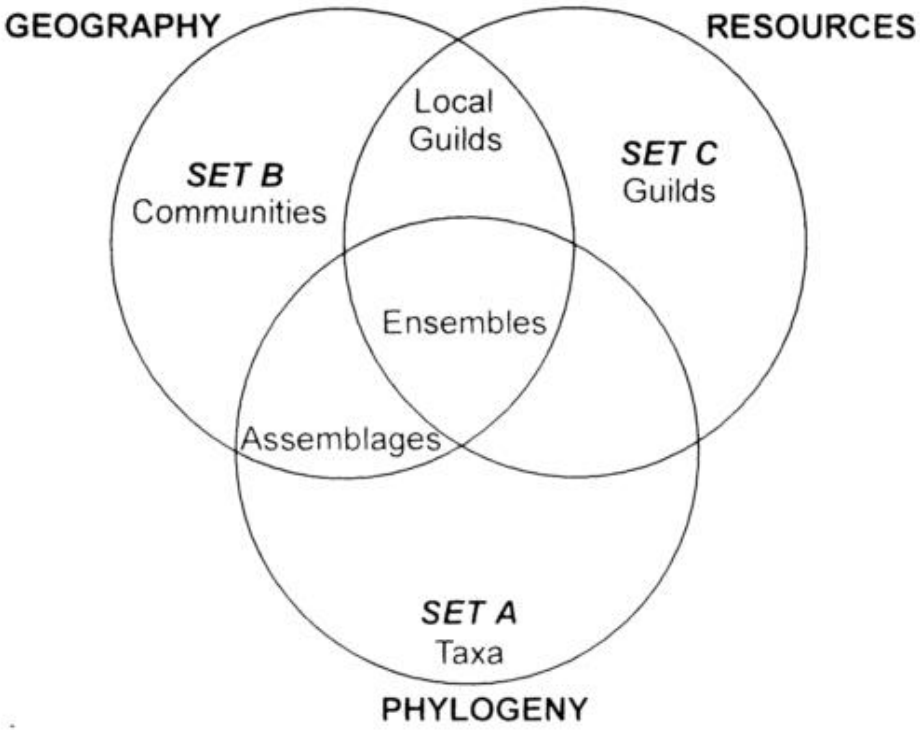


Figure 1. The conceptual framework suggested by Fauth *et al*. (1996), on how ecological units should be defined. These units are based on the suggestion that populations of species under study can be subdivided based on A) their phylogeny, B) their geographic location, or C) their resources. According to this model, an ecological "community" is a collection of species populations that are share a common time and place. Intersecting the concept of community with phylogeny and resource use gives us operational definitions for "assemblages", "guilds" and "ensembles". There is no term suggested for the intersection between phylogeny and resources because such phylogenetically restricted groupings of species using the same resource are usually described by specific compound descriptors of their taxonomic identity and resource use i.e. pond breeding salamanders.

1.2 Ecosystem capacity

Living things require energy to survive. The availability and flow of energy through an ecosystem determines its "capacity to support life" (Brown, 2014). An understanding of how the capacity of systems to support life (here on termed "ecosystem capacity") influences and is influenced by organisms is fundamentally important in understanding biodiversity patterns. In this section, I will explain how this broad concept is relevant to assessing biodiversity

change within assemblages, and what quantification methods are most appropriate for the questions I will ask in my thesis.

Ecosystem capacity is the product of two pathways of energy allocation in living systems (Connell and Orias, 1964). The first pathway is that of maintenance. This is the energy used for regulatory activities, which is the general process of living such as respiration and digestion. This energy is dissipated into the atmosphere as heat. The amount of maintenance energy used depends on the internal and external condition of the organism (Brody, 1945). The second energy pathway is that of productivity. This energy is used for non-regulatory activities includes growth, regeneration and reproduction. Energy used in productivity is stored as biomass. Because the energy from productivity is stored and available for other organisms to consume, I shall hereafter refer to it as "standing capacity" (**Figure 2**).

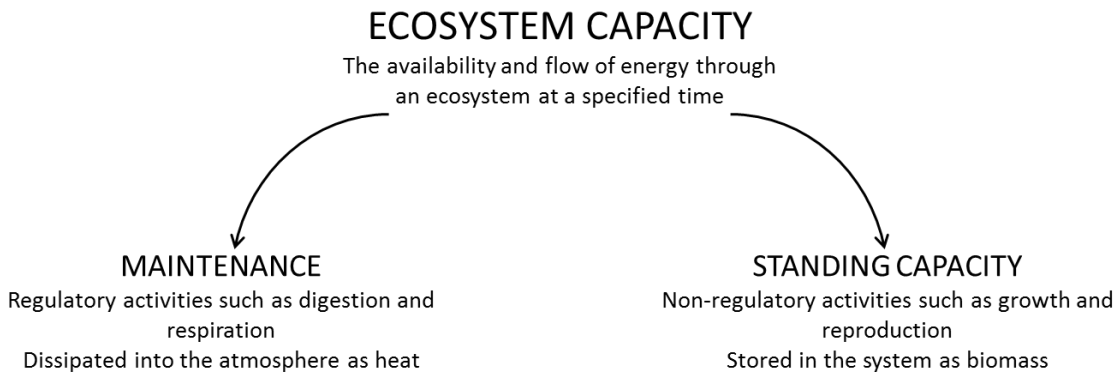


Figure 2. Energy is a basic requirement for life. How this energy is stored and made available to living things within an ecosystem can be considered the capacity of that ecosystem to support life, or "ecosystem capacity". There are two pathways of energy flow within an ecosystem at a given time. The first pathway is that of maintenance. All living things require energy for essential maintenance and regulatory activities such as digestion and respiration. Energy used for these activities is not stored within the ecosystem, but instead dissipated into the atmosphere as heat. Energy that is not required for maintenance can be used in non-regulatory activities involving growth, regeneration and reproduction. Standing capacity is the energy is stored in an ecosystem through productivity. It is stored in the form of biomass, and is available to for other living organisms to consume. The standing capacity of an ecosystem is a consequence of the overall ecosystem capacity and amount of energy required for essential maintenance, as only energy not required for maintenance can be converted to standing capacity.

1.2.1 What influences capacity?

There are two main aspects of an ecosystem that influence its capacity to support life: abiotic factors and biotic factors. Abiotic factors, such as the physical conditions and the availability of sunlight and water, affect what resources are available and how difficult these resources

will be to access. Biotic factors, relating to the presence and activities of the organisms present, affect how well resources are accessed and which resources are accessible. Individual species may become well adapted to using the widest possible amount of resources, and a wide variety of species may allow for a great variety of strategies for accessing resources. For example, the diversity of primary producers affects both standing capacity and decomposition (Cardinale *et al*., 2011; Hooper *et al*., 2012), and the diversity of an assemblage can influence productivity by affecting its ability to utilise limiting nutrients (Tilman *et al*., 1996). The presence of particular organisms can also affect what resources are available to other organisms in an ecosystem (Lawton and Jones, 1995; Sterner and Elser, 2002).

The efficiency of organisms in converting available energy into productivity affects the balance between maintenance and standing capacity, and so affects the amount of organic matter available for other organisms. This efficiency is variable, as it relates to metabolic rate (Brown *et al*., 2004). The metabolism is the process in which living beings transform the basic elements needed for life, such as energy and nutrients, into useful components. It is metabolism, therefore, that determines how much and at what rate species use resources. While most organisms use the same basic biochemical processes, metabolic rates vary. This metabolic rate directly influences life history attributes, population interactions and ecosystem processes such as rates of biomass production. Which aspects of an organism affect its efficiency at accumulating standing capacity has interested ecologists for decades. An early attempt by Lindeman (1942) described factors affecting the efficiency of energy transfer within an assemblage, which can be considered the ratio of productivity to maintenance energy because a less efficient organism would use more energy in regulatory processes and less in converting energy to biomass. This study discussed the efficiency of energy transfer through trophic webs, and concluded that the vegetative successional stage of the assemblage and the trophic level of an organism were highly influential. As an organism rises through the food web, the efficiency of energy transfer drops. In other words, a top predator is likely to have a lower ratio of productivity to maintenance energy per unit of energy consumed than an autotroph.

Abiotic and biotic factors often act in tandem, for example more stressful physical conditions cause organisms to lose more energy in regulatory activities (Brody, 1945). The favourableness of the environment, and therefore its capacity to support species, is affected

by the productivity of the system. The productivity of a system is constrained by fundamental limitations of living things, such as basic requirements for light for photosynthesis and water for cellular activity. However, there is an element of organismal adaption that enables some species to live and thrive in less favourable environments (Brown, 1988).

A particularly influential guild of species in relation to ecosystem capacity is the autotrophs such as algae and plants. They produce most of their energy directly from light through photosynthesis. Production by this method is called primary production, and it is what supports the other organisms of the food chain. Gross primary productivity (GPP), as defined by Fahey and Knapp (2007), is the amount of organic matter created by plants through photosynthesis per unit of ground area per unit of time. This value includes both maintenance energy and productivity. Net Primary Productivity (NPP) is defined as the amount of organic matter left over after maintenance activities (Fahey and Knapp, 2007). As autotrophs are the organisms that produce the organic matter heterotrophs require, the NPP of these organisms has an important influence on capacity.

Further discussion on the partitioning of abundances between species takes place in Section 1.3.3 *Assemblage structure*, and a discussion on how capacity relates to the species present within the assemblage takes place in Section 1.3.1 *Biodiversity and capacity*.

1.2.2 Measuring capacity

Capacity is rarely if ever quantified at the ecosystem level because collecting data on all organisms within an area is extremely challenging and rarely undertaken. In general, capacity is quantified at the assemblage level or below. Because my thesis focuses on how assemblages are changing, I will therefore concentrate the following review on assemblage level capacity.

The two aspects of capacity, the energy used in maintenance and the energy stored through productivity as standing capacity (**Figure 2**), require different quantification methods. Directly quantifying the amount of energy dissipated as maintenance is challenging, because it relies on direct quantifications of the metabolic rate of organisms within the assemblage. Ideally, metabolic rate would be quantified in terms of heat lost by direct calorimetry, thereby quantifying the amount of energy dissipated in all biological activities (Brown *et al*., 2004). Instead, metabolic rate is usually estimated from rates of uptake of carbon dioxide in plants and oxygen consumption in prokaryotes and eukaryotes. Most estimations of metabolic rate focus on basal rate, which is the minimal metabolic rate of an animal in a laboratory, but

actual *in situ* organisms' metabolic rates are usually two to three times basal rates (Brown *et al*., 2004). Many field studies cannot or do not quantify metabolic rate directly. Instead, they rely on the fact that metabolic rate is closely regulated by temperature and body size. Kleiber's empirical law of energy conversion (Kleiber, 1932) has been used for this purpose when the numerical abundance and biomass of organisms are known (i.e. Dornelas *et al*. 2011). A difficulty with this method is that an organism's metabolic rate can also vary during the day, between periods of different resource availability, or between different behavioural strategies.

Standing capacity is usually quantified in terms of the assemblage size because collecting enough data for quantifying community size is usually prohibitively difficult. There are two currencies for quantifying assemblage size: numerical abundance and biomass. Although both currencies are linked by being measurements of assemblage size, they are not equivalent (Magurran and Henderson, 2003; Morlon *et al*., 2009). Biomass is a measurement of how much productivity has taken place and how much biological resources are available for other trophic levels to feed upon. It is therefore a close approximation for resource allocation between species (White *et al*., 2007). Unlike biomass, numerical abundance focuses on counting numbers of individuals, and is much more closely linked to population dynamics and demographics than biomass (White *et al*., 2007). Individual size differences of organisms are not considered when quantifying assemblage size using abundance.

How numerical abundance and biomass relate is an important but currently unclear issue. At a global scale that focuses on mean body sizes and numerical abundance, a pattern emerges that suggests strong links. The energetic equivalence rule (Nee *et al*., 1991), also referred to as Damuth's Rule (Damuth, 1981), focuses on the fact that as organisms' body size increases, their density decreases. Specifically, the relationship between the body size and density of an organism is the inverse of the relationship between body size and metabolic rate (usually -3/4). This theory suggests that the amount of energy a species uses (although not its standing capacity) is invariant across species with different body sizes. This rule has been applied successfully across many taxa, including mammals (Damuth, 1981) and birds (Nee *et al*., 1991), and explains much variation between body size and densities of predator-prey interactions (Barnes *et al*., 2010). Although the energy equivalence rule has much empirical support on large scales, how well it describes local assemblage body size distributions varies. The relationship between numerical abundance and body size at the assemblage level scales

far less closely than predicted by energy equivalence (White *et al*., 2007). This lack of trend may be because energy-equivalence deals with maximum potential species abundances, whereas local abundances can vary substantially across species ranges. The strength of the energetic equivalence at large scales may also be a statistical property of assessing such a large range of body sizes (Isaac *et al*., 2013).

Because body size and population densities are fundamentally important properties of systems, understanding how numerical abundance and biomass relate remains an important goal for ecologists interested in assemblage dynamics. One avenue for exploration that has not been fully explored, and holds potential for elucidating this relationship, is assessing how numerical abundance and biomass change. I will address this knowledge gap in *Chapter 3*.

1.3 Measuring biodiversity

As biodiversity is such a complex concept, it is unsurprising that there is a plethora of different ways of quantifying it. Choosing the appropriate metric and scale for the question at hand is essential for effectively exploring biodiversity change. In this section I will provide an overview of a variety of methods used to focus on and measure different aspects of ecological assemblages. There are many ways of measuring assemblage biodiversity, but limited resources available to ecologists. Consequently, one of the aims of my thesis is to elucidate which of a selection of elements of assemblage biodiversity are most sensitive to change. By doing so, I hope to suggest appropriate metrics for detecting biodiversity change at the assemblage level.

1.3.1 Species richness

One of the most basic measurements of biodiversity is the number of species in an assemblage: species richness. This measurement has the advantage of simplicity, as only one element of diversity is considered. It is also the most intuitive index of community structure (Gotelli and Colwell, 2001). Species richness does not differentiate between species, so the identities or abundances of different species do not factor into quantifications. A very abundant species holds the same weight as a rare species, for example, and the presence of immigrating species can be overlooked (Lamb *et al*., 2009). This means species richness retains only a small amount of the overall information about that system (Magurran, 2004). Despite this lack of information, species richness is thought to capture much of the essence of biodiversity (Gaston, 1996), and consequently there is a long history of using this metric

of biodiversity to try and understand ecosystem functioning (i.e. Tilman *et al*. 2014) and prioritise biodiversity conservation (Myers, 1988).

Although species richness is popular among ecologists, there are some difficulties with its application. The main issue is that more species are detected as more sampling is undertaken. This property of species richness means sampling effort can strongly influence results, particularly because achieving a complete list of all species in a community or assemblage is very challenging (Longino *et al*., 2002). Species richness does not increase linearly with sampling effort, instead there is a curved relationship where species richness initially increases at a high rate and then tails off towards an asymptote (**Figure 3).** Asymptotes are, however, rarely achieved in ecological surveys due to the difficulties in compiling complete species lists.

The non-linear relationship between effort and species richness creates challenges for comparisons between samples. Estimations of species richness need to account in some way for sampling effort, otherwise any differences detected between samples may be an artefact of sampling effort. One method to account for potential sampling differences is rarefaction. Rarefaction traditionally works by down-sampling larger samples until they are comparable with the smallest amount of sampling effort in the samples of interest (Colwell *et al*., 2004; Gotelli and Colwell, 2001). This down-sampling can be based on the number of individuals sampled (individual-based rarefaction), for example the number of trees identified in a forest plot, or the number of pitfall traps (sample-based rarefaction), for example the number of pitfall traps set in a plot. A drawback with this methodology is that data are lost for samples that are downsized. However, new methodologies have been developed to allow extrapolation from rarefaction curves (Chao *et al*., 2014; Gotelli and Colwell, 2011). This rarefaction with extrapolation potentially allows for more effective comparison between samples without relying on information on rare species. The relative utility of rarefaction with extrapolation in monitoring biodiversity change requires further exploration, and so I will discuss this subject further in *Chapter 2*.

Another option for estimating the species richness of a sample is to use the parametric Michaelis-Menten (MM) equation. In this case, the MM equation extrapolates to the asymptote of the sample species richness (Colwell *et al*., 2004). This method does not require additional information on the sample in question. Alternatively, non-parametric models can be used that attempt to estimate the number undetected of species in the survey data, and

add this number to the number of species detected. Where there are numerical abundance data in addition to species presence/absence, the presence of singletons (species with an abundance of 1) in species accumulation curves is a strong indicator that unseen species are yet to be detected (Chao, 1984). Alternatively, the frequency of species that are recorded in only a single sample, called "uniques", can also be used to make inferences about undetected species (Chao, 1987). These models use statistical estimation approaches, including rarefaction with extrapolation, to deduce the number of unseen species in survey data (i.e. Gotelli & Colwell 2001; Gotelli & Colwell 2011; Chao & Jost 2012; Chao *et al*. 2009).

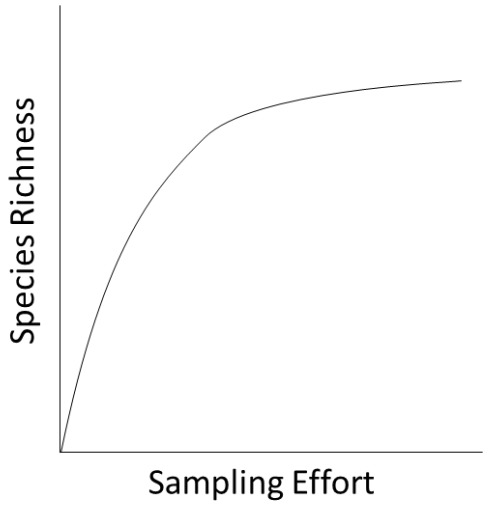


Figure 3. A visual representation of the species accumulation curve. With increased sampling effort there is initially a steep increase in species richness. At this point, many new species are discovered. Further increase in sampling effort does not increase species richness to the same degree as there is a gradual tailing-off of new species being discovered.

1.3.2 Assemblage structure

While species richness and assemblage size can both provide useful information on how assemblages are changing, they do not provide detail on assemblage structure. That the abundances of species within an assemblage vary substantially has been declared one of

ecology's few rules, because all assemblages have a few very abundant species and many rare species (McGill *et al*., 2007). In general, assemblages will be dominated by one or a few common locally abundant species, and there will be many locally uncommon species. In addition to overall assemblage size, the relative abundance of each species can also be integral to assemblage composition. Quantifying this property of how numerical abundance or biomass is distributed between species is called assessing assemblage evenness. An assemblage where species abundances are distributed uniformly is considered extremely even, with increasing deviations from this uniform pattern suggesting decreasing evenness. The obverse of evenness is dominance, which quantifies how much a single species dominates the assemblage size.

Quantifying evenness so that assemblage structure can be compared is challenging. The reason for this is that rare species are often missed in small samples, so the evenness of an assemblage will decrease as sampling effort increases. There are many different metrics available to quantify evenness, although not all are equally useful. Smith & Wilson (1996), for example, reviewed a total of 17 evenness metrics, and concluded that the different metrics produce quite different results when analysing the same data. This variability in evenness results is because not all evenness metrics meet the necessary criteria of being independent statistically from species richness. Instead, in many cases evenness decreases both with the marginal decreasing of rare species population and the addition of rare species, and that the evenness values depend continuously on the proportional abundance of any species (Routledge, 1983). The most appropriate metric for quantifying evenness is Hulbert (1971)'s probability of interspecific encounter (PIE), because it is one of the few diversity metrics that can be interpreted in biologically meaningful ways (Gotelli and Graves, 1996).

Evenness and species richness combine to describe the diversity of an assemblage (Hill, 1973). Various diversity metrics have been developed to combine these two concepts statistically, such as the commonly used Shannon's Entropy (Shannon, 1948) and Simpson's Diversity Index (Simpson, 1964). The Shannon-Weaver Index has a long history of use in ecological studies since the 1950s (i.e. MacArthur 1955), and it measures the amount of variation among abundance values. The Simpson's Index assigns more weight to commoner species, and is therefore a measure of dominance. In both cases, evenness can also be derived by dividing the diversity value by species richness (Pielou, 1966).

Although these diversity metrics have proved popular in the past, their use causes some difficulties of interpretation. Both indexes relate the number of individuals of a species to the total number of individuals found and assume a randomly sampled and complete list of species. This is a problem, because situations that break this assumption are very common in community ecology. Another concern with these diversity metrics is that they confound the effects of species richness and evenness. The Shannon-Weaver Index also assigns them unequal weights (Strong, 2016). In addition, both the Shannon-Weaver and the Simpson's indexes lack two important mathematical properties: 1. monotonicity and 2. proportionality (Van Strien *et al*., 2012). This means that 1. when all species in a sample decline, the diversity indexes do not necessarily decline as well, and that 2. if all species abundances within a sample are changed by a given factor, the diversity indexes do not change by the same factor. These diversity indexes have therefore been demonstrably less sensitive to change than species richness (Lamb *et al*., 2009). In some cases the diversity indexes can even provide counter-intuitive results when monitoring change: for example they increase as common species decline but abruptly change if these common species decline to extinction (Santini *et al*., 2017).

The Hill number framework was developed to incorporate the various diversity metrics into a single system (Hill, 1973; Jost, 2006). The various Hill numbers differ by an exponent q, which determines the sensitivity of the metric in question to relative abundances of species. Species richness, for example, is equivalent to Hill number 0, because it does not consider species abundances. The Shannon and Simpson's indexes can also be transformed into Hill numbers by simple algebra. In this way, Hill numbers incorporate information on relative abundances and species richness of samples.

An alternative method of measuring community structure is to focus on species abundance distributions. These distributions can be plotted using a variety of methods. When plotted as histograms of the number of species on the x axis, and binned abundances on the y axis, all assemblages show a "hollow curve" shape where a few species are common and many species are rare species (McGill *et al*., 2007). Variability in the structure of assemblages becomes evident when abundance distributions are plotted in other ways.

A common choice for visualising species abundance distributions is the rank abundance Whittaker plot (Whittaker, 1965), which is a rank abundance plot that plots species ranks against relative or actual abundance (**Figure 4A**). This plot type is useful because it clearly

visualises differences in species richness patterns and highlights differences in evenness between assemblages (Magurran, 2004; McGill *et al*., 2007). It is less useful, however, in comparing the species abundance distribution of two assemblages with very different species richness because it is so highly influenced by the overall number of species (McGill, 2011).

An alternative way of plotting species abundance distributions is to plot histograms of the frequency of species in different logged or unlogged abundance classes (**Figure 4B**). These plots are often called Preston plots because they were first used in Preston (1948). There has been a substantial amount of controversy around the use of histograms like Preston plots, however, because different binning methods can influence the histogram's shape (McGill, 2011). The interpretation of the number of rare species, for example, depends on whether the arithmetic or logarithmic scale is used. On one hand, binning represents the loss of data, which is usually best avoided. On the other hand, binning can be useful when visually comparing distributions of numerical abundance and biomass.

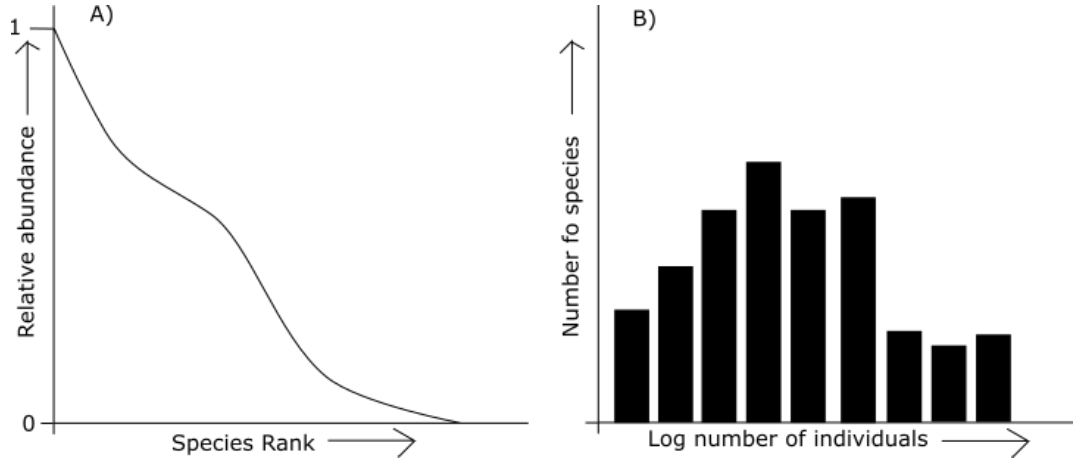


Figure 4. The two main ways of visualising species abundance distributions: a Whittaker rank abundance curve (A) and a Preston plot histogram of species frequencies.

There are two main species abundance models for describing species abundance distributions: the log series model and the log normal model. The log series abundance model developed by Fisher *et al*. (1943), was originally a description of empirical data. This model predicts that the greatest number of individuals will be found in only a one or a few species populations (**Figure 5A**). The numbers of individuals per species population is far lower for

the rest of the species in that assemblage, so that there is a small number of common species and a large number of rare species. Even on a log scale, this pattern of one or a few species dominating the assemblage size is evident. This model has largely been associated with highly disturbed, unstable or early successional assemblages (Ulrich *et al*., 2010).

The other model, first developed by Preston (1948), is the log normal abundance model (**Figure 5B**). Unlike the log series model, the log normal model predicts that there will be a small number of species with few individuals, a large number of species with intermediate numbers of individuals and few species with large numbers of individuals. This model is more closely associated with more stable, mature assemblages that are influenced by a large variety of ecological factors (Ulrich *et al*., 2010). There is the potential, however, for the logseries model to arise due to insufficient sampling of a log normal distribution (Magurran, 2004), because there may be many very rare species that are not detected by sampling methods.

Attempts have been made to assess whether most assemblages better fit a logseries or log normal abundance distribution. For example, a meta-analysis of over 550 species abundance distributions by Ulrich *et al*. (2010) failed to reach a decisive conclusion, although they found that more assemblages fit the log-normal distribution. Species abundance distributions are also often multimodal, especially al larger spatial scales or taxonomic breadth (Antão *et al*., 2017). The species abundance distribution within an assemblage can also change over time (Magurran, 2007). As assemblages become increasingly disturbed, they generally show a shift towards a logseries shaped abundance distribution as rare more vulnerable rare species are lost (Mouillot *et al*., 2013). As yet, we do not know how assemblages are changing in general in response to increasing anthropogenic pressures. A better understanding of how different elements of the abundance distribution, such as dominant and rare species, change over time is needed to clarify this issue.

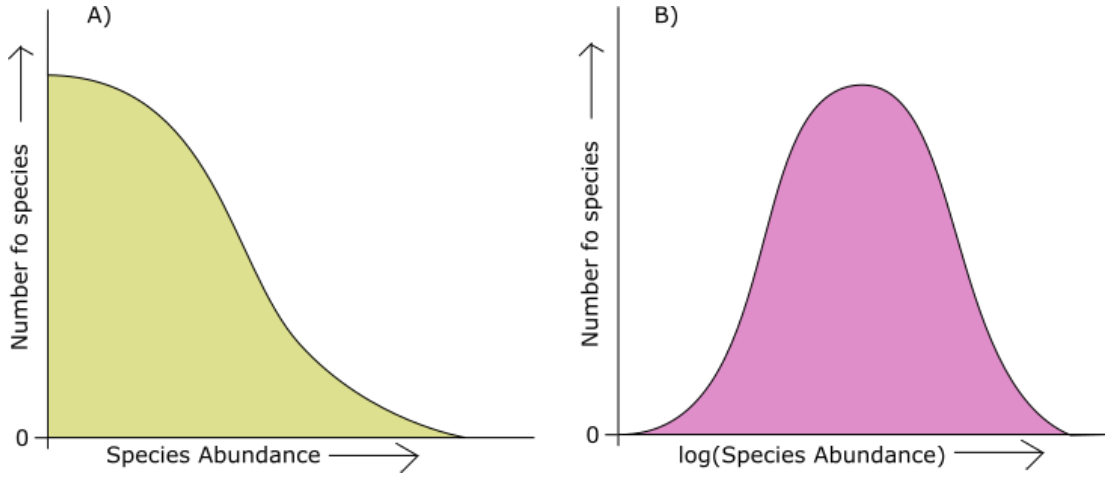


Figure 5. The two main modes predicted to fit the species abundance distributions of natural assemblages: the logseries (A) and the lognormal (B). Both models are displayed as they appear in Preston plots.

1.2.5 Turnover

As mentioned in Section 1.3.1 *Spatial scale*, biodiversity can be partitioned into different scales. Beta diversity refers to the difference between two assemblages, and so quantifies turnover. This turnover can refer to spatial or temporal differences. Two assemblages are considered compositionally identical only if they have the exact same species and relative abundances (Jost *et al*., 2011), although this situation is highly unlikely to happen in natural systems.

There are a set of metrics designed for assessing turnover between assemblages. Some metrics only consider species identities, and so ignore structural changes within an assemblage. Commonly used examples of such metrics include the Jaccard index and the Sørensen index. The Jaccard index compares the number of shared species to the total number of species across both assemblages, whereas the Sørensen index compares the number of shared species to the mean number of species in an assemblage (Jost *et al*., 2011). These incidence-based metrics are attractive when assessing turnover because only presence-absence data is needed. A potential shortfall with their use, though, is that we rarely have complete species lists for assemblages, so turnover may be inflated by incomplete sampling. In addition, although they are affected by change in species richness which is influenced by changes in the species abundance distribution, incidence based turnover metrics do not directly detect changes in assemblage structure.

Other metrics are available to quantify turnover that also include species relative abundances: for example the Morisita-Horn index (Jost, 2006; Morisita, 1959) and the Bray-Curtis index (Bray and Curtis, 1957). The Morisita-Horn index is highly dominated by the most abundant species because it is based on the squared differences of the relative abundances of each species. The Bray-Curtis index is closely linked to the Sørensen, and in fact reduces to the Sørensen index when all species in each assemblage are equally abundant. When abundances are not identical, it compares the difference between the smaller and larger abundance value for each species. Although this index is widely used in ecology, it confounds density with compositional similarity (Jost *et al*., 2011). This is a problem if the assemblage size of the assemblages under comparison differs, because a species may then have the same relative abundance but a very different observed abundance.

Turnover can also be partitioned into two different phenomena: nestedness and true turnover (Baselga, 2010). Nestedness of assemblages is when the biotas of assemblages with a smaller number of species are a subset of assemblages with a greater species richness. "True" turnover, on the other hand, refers to species replacement, where some of the species in one assemblage are replaced by different species in another assemblage. The nestedness component of turnover, then, is influenced by changes in the species richness of assemblages, whereas turnover in terms of species replacement is not.

Choosing the most appropriate turnover metric depends on the question at hand and the types of data. Because abundance methods by definition consider changes in abundance as well as species identity, and are less sensitive to incomplete samples, for some questions they can provide more ecologically meaningful and informative approaches (Jost *et al*., 2011). When rare species are of particular concern, however, metrics that focus strongly on common species such as the Morisita-Horn index may be less appropriate. In these cases, incidence-based indexes may be a better choice because they are more sensitive to changes amongst rare species. Different types of index can also be used in tandem. For example comparing results of incidence vs abundance based turnover indexes can provide information on whether the turnover in assemblages is predominantly taking place amongst the rare or dominant species (Hillebrand *et al*., 2008).

Turnover indexes were generally developed for spatial turnover, but there are few issues with applying them to the question of temporal turnover (Magurran, 2011). One problem that must be considered, though, is that more species are found over time as sampling

progresses. Over time, samples display increasing species-time curves, where more species are detected as time progresses in a similar way that samples over space display a species-area curve (Preston, 1960). The difference between assemblages is also a function of the time period between samples (Diamond and May, 1977). Plotting turnover values against census intervals is the simplest approach to dealing with this problem (Magurran, 2011).

1.4 What contributes to biodiversity?

What contributes to the diverse array of life we see on earth is a complex question that has intrigued ecologists and natural historians for many years (Chave *et al*., 2002). In the long term (millennia), evolution is responsible for the breadth of species we see today. In the shorter term, however, how diversity is maintained within assemblages when most species are rare (McGill *et al*., 2007) remains unclear. Because natural systems are complex, there are likely many different mechanisms contributing to biodiversity.

Despite attempts to alleviate biodiversity loss, negative trends in biodiversity persist (Butchart *et al*., 2010). Extinction rates are so high that we may be entering a 5th, anthropogenic, mass extinction (Barnosky *et al*., 2011; Chapin *et al*., 2000; Naeem *et al*., 2012). A large amount of genetic loss within species has also been recorded, and further losses are possible (Bálint *et al*., 2011). Understanding biodiversity loss is important because it is a major driver of ecosystem change (Hooper *et al*., 2012). However, biodiversity change is also commonplace in many systems (Dornelas *et al*., 2014), and the implications of change are currently unknown in many cases.

How species richness is changing is often used as a general proxy for biodiversity change (Isbell *et al*., 2017). Although species richness is declining in highly disturbed habitats (Murphy and Romanuk, 2014; Newbold *et al*., 2015), there is no systematic trend in species richness over time in habitats that have not been substantially transformed (Dornelas *et al*., 2014; Vellend *et al*., 2017, 2013). This result does not mean that ecosystems are not being affected by increased anthropogenic disturbance, however, because many other aspects of an assemblage can change while species richness remains invariant (Spaak *et al*., 2017; Supp *et al*., 2012). Assessing biodiversity at a local scale is more complicated than monitoring a single aspect of assemblage biodiversity such as species richness (McGill *et al*., 2015). Changes in relative abundances, species identities and functional traits can occur without

changes in species richness, and are potentially highly influential for ecosystem functioning (Hillebrand *et al*., 2017).

Below I provide an overview of some of theories that are most relevant to assessing how assemblages are potentially changing in response to recent pressures. To begin with, I discuss the theories that predict how much biodiversity a system can support (Section 1.3.1 *Biodiversity and capacity*), and how relatively stable amounts of life may be supported even under changing conditions (Section 1.3.2 *The maintenance of assemblage functioning*). I then discuss mechanisms for maintaining a varied assemblage structure (Section 1.3.3 *Competition, exclusion, and assemblage structure*; Section 1.3.4 *Transient species*). Finally, I consider the potential consequences of biodiversity change on the overall breadth of variety within systems (Section 1.3.6 *Biotic Homogenisation*).

1.4.1 Biodiversity and capacity

How biodiversity and capacity interact is a contentious issue, with two conflicting theories proposed (**Figure 6**). The species-area theory, developed by MacArthur & Willson (1967), stated that species richness will be higher on large islands because a greater area means more individuals supported, and consequently lower extinction rates. The species-energy theory was developed by Wright (1983) to incorporate energy use into the species-area theory. This species-energy theory predicts that the overall capacity of an ecosystem is a limiting factor of species richness, and therefore biodiversity should increase with increasing energy availability (**Figure 6A**). Smaller islands support fewer species because they generally supply less overall energy than large islands, not because there is less space for species. The explanation Wright provides for the species-energy relationship is that higher resource availability allows species to maintain larger populations, thereby buffering more species from extinction. This aspect of this theory relating to demography is the More-Individuals Hypothesis (Srivastava and Lawton, 1998), where larger population sizes across all the species in an assemblage buffer species from extinction. The evidence for this theory is mixed. Wright (1983) applied his model to global data on freshwater birds and terrestrial angiosperms, and found that model accounted for 70-80% of variation in species richness. Some subsequent studies have also found positive trends between assemblage species richness and productivity (Gillman *et al*., 2015; Gillman and Wright, 2006). However, other studies find little evidence for the More-Individuals Hypothesis aspect of the energy-richness theory, either because the energy-richness relationship was not positive (McGlynn *et al*.,

2010), or the positive relationship is more closely related to the evolutionary rate in higher energy systems (Evans and Gaston, 2005).

An alternative, non-linear, relationship between capacity and species richness has also been suggested. A unimodal relationship between increasing capacity and species richness was proposed by Huston (1979) through the competitive exclusion theory (**Figure 6B**). This theory, related to the intermediate disturbance theory (Section 1.3.3.2 *Intermediate disturbance hypothesis*), proposed that the hump-shaped relationship of species richness with increasing assemblage size is a consequence of different rates of competition within assemblages. Competition is highest at an intermediate energy-availability, because in very high energy-availability systems a few species can become sufficiently dominant that they outcompete many more uncommon species. There is empirical evidence for this relationship in a variety of assemblages. For example, the unimodal relationship fit assemblages of tropical ants better than a positive relationship (McGlynn *et al*., 2010), and an analysis of vegetation biomass found evidence for this unimodal relationship between energy and species richness in multiple assemblages (Fraser *et al*., 2015). The authors suggested, however, that the high productivity-low species richness section of the curve where biodiversity decreases with increasing capacity may be because very high diversity grasslands tend to be more highly modified by humans.

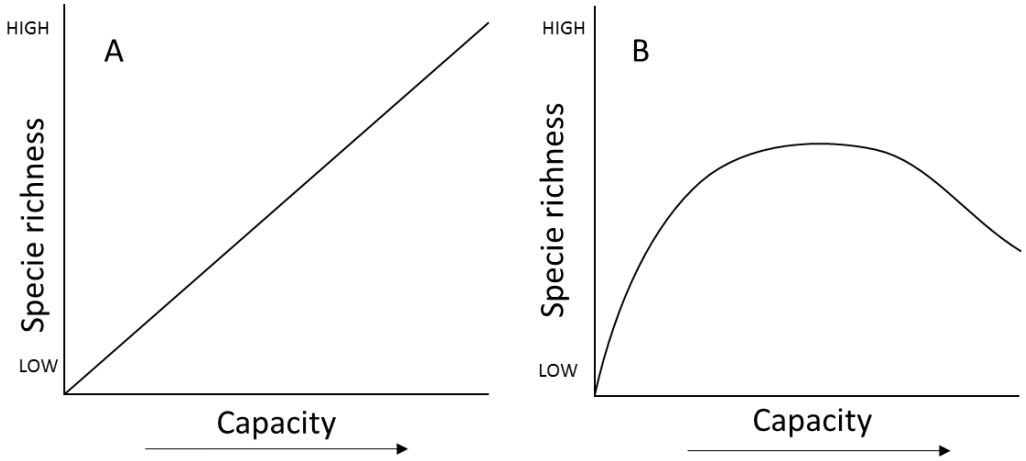


Figure 6. The Species-Energy Theory predicts that species richness increases linearly with increasing capacity (A). Systems with higher overall energy availability can support more life. Through the More Individuals Hypothesis, more capacity leads to more individuals for each species, which in turn reduces the probability of local extinctions for each species. The alternative capacity-species richness theory predicts a curved, unimodal, relationship (B). This theory assumes that successful species can more easily gain a monopoly over less successful species when capacity is high. Systems with intermediate capacity are not conducive to species monopoly, so more species can coexist within the same community. In forests, for example, large trees can shade out competing undergrowth species more effectively than intermediately sized trees, thereby causing fewer undergrowth species to survive.

Attempts have been made to generalise relationships between capacity and species richness. A review by Mittelbach *et al*. (2001) did not find a single general pattern; the patterns depend on scale and taxa. For example, animal assemblages tended to have linear increasing relationships, whereas plant assemblages tended to have unimodal relationships. An analysis by Partel *et al*. (2007) suggested that tropical ecosystems were more likely to have positive linear relationships between capacity and species richness, whereas temperate ecosystems were more likely to display a unimodal relationship. A study by Šímová *et al*. (2013) on plant communities found no universal species richness-capacity relationship. The authors explain this result by claiming that species richness is a product of many interacting factors in addition to capacity, such as individual abundance and habitat heterogeneity.

One of the reasons why the relationship between capacity and species richness may be proving difficult to quantify is that studies do not directly measure ecosystem capacity; instead they tend to assess assemblage standing capacity in terms of assemblage size. Even then, different currencies can be involved, with various quantifications of numerical

abundance and biomass used. Such variation in quantification is potentially obscuring patterns because different currencies of assemblage size are not equivalent (Morlon *et al*., 2009). When developing the species-energy relationship theory, Wright (1983) specified energy in his model as the rate at which resources that available to the species of interest are produced. This definition is a product of overall ecosystem capacity and maintenance efficiency of the assemblage, and so would be measured as the assemblage size according to my conceptual model (**Figure 2**). Appropriate proxies for energy availability for the species-energy relationship depend on the taxa of interest, for example solar radiation for primary producers or biomass production for secondary producers.

Another issue when attempting to understand the relationship between capacity and species richness is that both ecosystem and assemblage standing capacity are in part a function of species richness. Relationships may therefore be complex. Species richness can be considered either the dependent or independent variable in relation to capacity (**Figure 7**). One example is a study by Dornelas *et al*. (2011) which considered species richness as the independent variable (**Figure 7A**). The results of this study indicated that as species richness increases, there is on average a small increase in assemblage size.

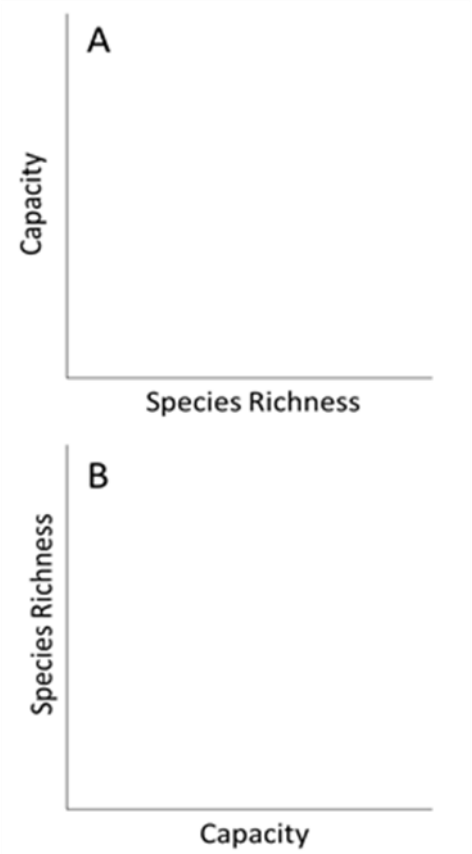


Figure 7. Whether species richness should be considered the independent (A) or dependent (B) variable in relation to assemblage size is unclear. The relationship can be considered as either scenario A or B, but which scenario is chosen has implications for the type of research questions asked. Both the theories linking capacity to biodiversity in **Figure 6** assume relation B.

A further complication in the relationship between biodiversity and capacity is that the relationship may not be direct. Cardinale *et al*. (2009) suggested that it is the amount and balance of resources available that influence species richness, not capacity *per se*. They proposed a new multivariate theory to explain species richness patterns which includes ratios and overall quantities of limiting resources, biomass production by potentially competing species, and the number of species co-occurring within a community.

To better understand how biodiversity and capacity relate, we need a deeper understanding how variable capacity is, how different currencies to measure capacity influence results, and

whether there are systematic shifts in the overall amount of capacity within local systems. In my thesis, I aim to address questions related to shifts in standing capacity in terms of assemblage size rather than ecosystem capacity, because local scale surveys most often quantify either numerical abundance or biomass rather than directly measuring energy flow. In *Chapter 3*, I will therefore ask questions about how different currencies of assemblage size (numerical abundance and biomass) relate at the assemblage level. In addition, I will test for evidence of systematic trends in assemblage size across systems.

1.4.2 The maintenance of assemblage functioning

Various mechanism have been suggested to explain how assemblage level properties can be maintained despite substantial disturbances and change within assemblages (Cardinale *et al*., 2012). One theory about how populations of species within assemblages change is based on compensatory dynamics (Tilman *et al*., 1998), where changes in population abundance are primarily driven by changes in the abundance of co-occurring competitors. When compensatory dynamics take place, average species abundances will co-vary negatively (Houlahan *et al*., 2007). Such compensation suggests substantial reordering of the assemblage structure (Gonzalez and Loreau, 2009). For compensatory dynamics to maintain assemblage size stability, there must be a variety of different responses to pressures applied to the assemblage. There must also be the opportunity for compensatory extinctions and immigrations (Brown *et al*., 2001), although to some extent compensatory dynamics can take place without species turnover (Gonzalez and Loreau, 2009). Higher species richness, and therefore a higher chance of functional diversity, is predicted to increase ecosystem stability because there are more potential responses amongst species (Wang and Loreau, 2016)

While the theoretical basis for compensatory dynamics has received much attention, the empirical evidence for this theory is conflicting. Evidence for compensatory dynamics after disturbance has been found after assemblages undergo disturbance (Steiner *et al*., 2011), and has been noted in both disturbance-sensitive and disturbance-tolerant species (Keitt, 2008). Conversely, a meta-analysis of 41 different plant and animal assemblages found little evidence for the negative covariance of populations that is predicted by compensatory dynamics (Houlahan *et al*., 2007).

An alternative explanation for the maintenance of assemblage level properties under changing conditions is the portfolio effect. This theory, based on portfolios of products with financial risk, stipulates that aggregate systems are less volatile than their component parts

(Schindler *et al*., 2015). As with compensatory dynamics, the portfolio effect predicts greater stability in assemblages with higher diversity. The key difference between these concepts, however, is their explanation for the underlying mechanisms. In compensatory dynamic species population trends should negatively co-vary, whereas in the portfolio effect population trends should not co-vary. Ecosystem properties are maintained through statistical properties, not species interactions (Doak *et al*., 1998). This does not mean the portfolio effect predicts that assemblages will remain stable irrespective of the drivers of change, because habitat homogenisation and restrictions on animal movement decrease the possibility that the variation among species is sufficiently great to deliver adequate portfolio effects (Schindler *et al*., 2015). Asynchronous dynamics, where species react differently to drivers of change due to different ecological niches, are evident in many temporal studies (Houlahan *et al*., 2018; Magurran and Henderson, 2010). The portfolio effect, however, does not necessarily act exclusively to maintain assemblage stability. There are many empirical examples of compensatory dynamics and the portfolio effect both contributing to stability (Mikkelson *et al*., 2011).

Both compensatory dynamics and the portfolio effect suggest that assemblage level properties may be maintained despite substantial biodiversity change. We currently do not know how often assemblage size, which is a fundamentally important assemblage property, changes directionally rather than being maintained at a relatively stable value. As mentioned in the section above, I will address the knowledge gap of how common directional change in assemblage size is in *Chapter 3* alongside testing how closely change in the currencies of numerical abundance and biomass relate.

1.4.1 Spatial scale

There are three different scales that biodiversity can be measured at: alpha, beta and gamma scale diversity (Whittaker, 1960). Alpha diversity is the diversity of a single assemblage or community (**Figure 1**). Beta diversity is the compositional diversity between areas of alpha diversity, and can be assessed in terms of spatial or temporal turnover. Gamma diversity is the diversity of a large geographic region, and is a combination of alpha and spatial beta diversity. How biodiversity is measured within these scales varies, as does the patterns of diversity within them.

The spatial scale at which biodiversity change is assessed can affect the detected trend (McGill *et al*., 2015). At the global scale, biodiversity is decreasing, as evidenced by the high

number of extinctions taking place (Ceballos *et al*., 2015). At smaller spatial scales, however, the picture is less clear. Issues of scaling have been recently debated in relation to detecting species richness change (Primack *et al*., 2018). In contrast to the consistent evidence of declining global species richness as increasing extinctions occur, the evidence for declining local species richness is mixed. Some studies found no trends in local species richness (Dornelas *et al*., 2014; Vellend *et al*., 2017, 2013), while others find evidence for a general decline in species richness (Newbold *et al*., 2015). Because species richness trends vary between local and very large scale assessments (Chase *et al*., 2019), predicting trends at one scale from trends at another is difficult. Scaling is also not just an issue for species richness. Other ecological relationships and patterns are also scale dependent, including the species-energy relationship (Evans *et al*., 2005), the ratio of native to exotic species (Peng *et al*., 2019), biodiversity-ecosystem functioning relationships (Brose and Hillebrand, 2016), and species abundance distributions (Antão *et al*., 2017). Care needs to be taken regarding choosing appropriate spatial scales when assessing biodiversity change. To this end, I will focus on local species assemblages in my thesis analyses.

1.4.3 Competition, exclusion, and assemblage structure

How different species coexist in the same assemblage or community is a fundamental question underpinning biodiversity. As I mentioned in Section 1.3.3 *Assemblage structure*, assemblages generally contain one or a few very abundant dominant species, and many less abundant species (McGill *et al*., 2007). To maintain diversity within assemblages, then, mechanisms must exist to avoid the most abundant species competitively excluding all other species. Systematic shifts in the relative abundance of these very abundant dominant species could consequently indicate changes in the underlying mechanisms supporting diversity within assemblages. Below I provide an overview of some of the most influential proposed mechanisms underpinning the species abundance distributions found in natural assemblages: niche partitioning, the intermediate disturbance hypothesis, and density dependent and independent mortality. In *Chapter 4* of my thesis, I then test whether there are systematic shifts in the absolute and relative abundance of dominant species across assemblages.

1.4.3.1 Niche partitioning

Niche partitioning is one explanation for species coexistence which attempts to explain how resources are shared between species. A niche is the specific range of conditions a species can tolerate (Huston, 1994). The “fundamental niche” is the potential distribution of species

in the absence of competition, and so represents the potential ecological space a species takes up (Brown, 1981; Hutchinson, 1959).

Many different aspects of an organism's ecology affect its ecological niche, including trophic level, body size, mobility and stress tolerance. In its essence, niche theory suggests that ecosystems contain many different niches, thereby allowing many species that are adapted to different niches within the same system to co-exist. Niche breadth is also variable between species. Some species may have very narrow fundamental niches because they specialise strongly in a particular habitat or resource. Other generalist species may have very wide fundamental niches because they can utilize a wide variety of habitats or resources. There is a trade-off for species between efficiency vs breadth of resource utilisation, where specialists are likely to be better than generalists at using a particular resource but generalists can access more resource types (MacArthur *et al*., 1972).

Most species compete with each other, and so do not fill their entire fundamental niche, because they are excluded from some parts of their niche by other species. This narrower niche type, where competition due to overlapping niches is considered, is called the "realised niche" (Hutchinson, 1959). How species coexist through niche-partitioning is a difficult question to answer, because the factors influencing ecological space are very variable. However, due to species exhibiting realised niches rather than fundamental niches, interspecies competition and mechanisms that regulate such competition will play an important role.

1.4.3.2 Intermediate disturbance theory

An influential but controversial theory relating disturbance to biodiversity is the Intermediate Disturbance Hypothesis (IDH). This theory, originally proposed by Connell (1978) in relation to tropical forests and coral reefs, has been included in many studies (Fox, 2013). The IDH predicts that assemblages are most diverse when they undergo intermediate frequency or intensity disturbances or environmental changes (**Figure 8**). An assemblage that reaches equilibrium cannot sustain as many species because highly competitive species will dominate the system to too great an extent. Assemblages rarely reach equilibrium; most assemblages experience disturbances of varying pressure and frequencies. In such assemblages, the competitively superior species will rarely reach abundance levels that allow for competitive exclusion of other species because the disturbances will set back the process by killing or damaging individuals (Townsend *et al*., 1997). This theory is built upon three premises: 1.

Disturbances reduce species densities, 2. Intermediate disturbances reduce all species densities so that all species have the subsequent opportunity to increase in density, and 3. No species will have time to increase in population quickly enough to exclude other species (Fox, 2013). Empirical evidence for the IDH is substantial, with IDH found in a wide variety of taxa and systems (e.g. Scotti *et al*. 2015; Lee *et al*. 2011; Townsend *et al*. 1997).

The validity of this theory has, however, recently being questioned, with Fox (2013) going so far as to call for the IDH to be abandoned. The empirical evidence was questioned because systems displaying the IDH were less common than expected (Hughes *et al*., 2007; Mackey and Currie, 2001). More importantly, Fox (2013) questioned the logic of the three fundamental mechanisms underpinning the IDH. The first issue Fox (2013) took with the IDH is with the assumption that intermediate disturbance decreases species densities, thereby decreasing competition. The issue with this mechanisms is that disturbance also decreases the amount of competition needed to cause competitive exclusion (Chesson and Huntly, 1997). Another issue Fox (2013) took with the IDH is the assumption that intermediate disturbance prevents a system from reaching "equilibrium" by temporarily reducing all species to low population levels. The problem in this case is that it is the increase in average mortality rates rather than the increase in disturbance *per se* that causes this effect. The third issue Fox (2013) had with the mechanisms underpinning the IDH is the assumption that temporally shifting environmental conditions causes different species to be dominant at different times, thereby inhibiting a single species from dominating the system to the exclusion of all other species. While spatial environmental variation can allow different species to be dominant in the most favourable areas, temporal environmental variability does not allow this. Instead, a species must be able to grow and compete equally well under all conditions it experiences. A reply by Sheil & Burslem (2013) acknowledged that the IDH is vulnerable to misuse, but rejected the conclusion by Fox (2013) that the IDH should be abandoned. When considered in a narrow definition, they believe that the IDH is still relevant specifically to complex sessile communities. In these assemblages, disturbance would be low at late successional stage sites without IDH, because early-stage disturbance-dependent species would be outcompeted by the later stage species.

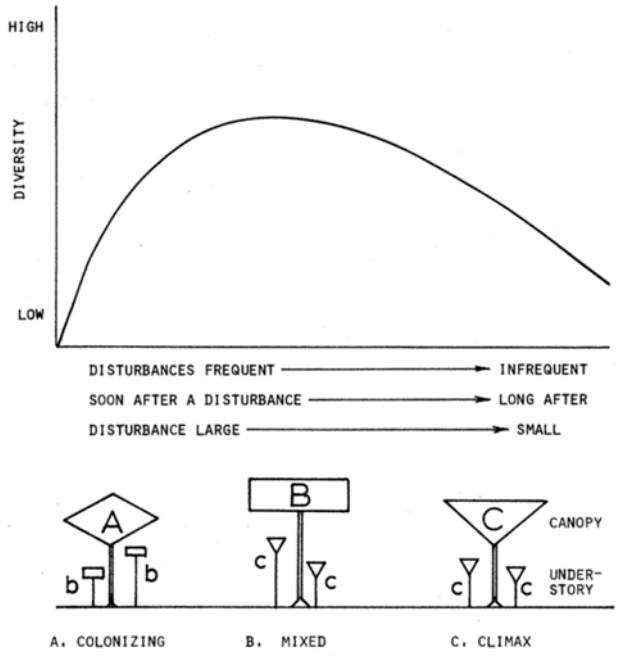


Figure 8. A graphical illustration of the intermediate disturbance theory (IDH), taken from Connell (1978). Species diversity is predicted to be greatest in ecosystems where disturbance is at an intermediate level. The example given below relates the IDH with forest successional species.

1.4.3.3 Density dependence and independent mortality

A key concept in explaining assemblage composition and the maintenance of biodiversity is the r/K species continuum. This theory, first proposed by MacArthur & Willson (1967) in their theory of island biogeography, relates to how the types of selection species undergo is dependent on the resources available to them. The main mechanism underpinning the r/K species continuum how strongly species undergo density dependent mortality. This mortality takes place when individuals of a species are at so high a density that they compete with each other and so mortality occurs. This mechanism is contrasted to density independent mortality, where external factors act upon species populations, causing mortality that is unrelated to interspecific competition.

In the theory of r/K species, a distinction is made between the most successful traits selected for in disturbed vs more stable environments (Reznick *et al*., 2002). When irregular

disturbances such as temperature fluctuations cause frequent population declines, species undergo density-independent mortality. Resources are subsequently abundant, so species that can reproduce fast and so take advantage of this resource availability will outcompete species with much slower growing populations. Such species put maximum available resources into reproduction, and the smallest amount of energy possible into each offspring (Pianka, 1970). These species with a high capacity for population increases are termed "r-selected" species after a parameter from the logistic equation for per capita population grow rates when population size is near zero (MacArthur and Willson, 1967; Reznick *et al*., 2002). In more stable environments, species populations are much closer to using all available resources, and so are closer to their carrying capacity. Species in these cases will experience substantial density dependent mortality as individuals compete for limited resources. In this case, the optimal strategy is to focus energy on maintenance and producing a few very fit individuals who can compete successfully (Pianka, 1970). Because they are controlled by the carrying capacity of a system, species with this life history strategy are termed "K-selected" after the parameter for carrying capacity (MacArthur and Willson, 1967; Reznick *et al*., 2002). Species life strategies fall on a continuum between r-selected and K-selected strategies (Reznick *et al*., 2002). Different species within the same community or assemblage can also favour different life history strategies.

The theory of the r/K continuum predicts that organisms in more disturbed conditions are likely to be smaller and reproduce faster. As assemblages are under increasing pressures from anthropogenic disturbances globally, this theory consequently predicts a general decrease in body size across assemblages. I test this theory in *Chapter 4* by focusing on declines in body size of the dominant species within a selection of widely distributed assemblages and habitats.

A further development in the theories regarding density dependence and community structure relates to the trade-off between conspecific negative density dependence and intraspecific competition. Conspecific negative density dependence is when the presence of individuals from the same species causes greater density dependent mortality than the presence of other species. For example, individuals may be strongly affected by species-specific pathogens or predators that only pose issues when there are enough densities of target organisms. Such disproportionally strong density dependence can theoretically cause rarity (Chisholm and Muller-Landau, 2011; Yenni *et al*., 2012), and rare species have

empirically been documented displaying high conspecific density dependence (Mangan *et al*., 2010). Such species can maintain populations despite low numbers because they generally also have high reproductive capacity at very low abundances (Yenni *et al*., 2012). By this mechanism, the negative density dependence theory provides an alternative explanation or the persistence of species to that of the intermediate disturbance hypothesis, because it provides an expectation for rare but persistent species within assemblages. This theory casts doubt on the assumption held by many that rare species are more vulnerable to extinction than common species because of their low population sizes (Pimm *et al*., 1988). Low population numbers are often used as a proxy for extinction risk in conservation assessments (i.e. IUCN, 2001), so doubt upon this assumption has potentially important implications for conservation prioritisation as well as our understanding of how biodiversity is maintained within assemblages. Consequently, there is a need to systematically assess whether there are changes in the number of rare species within assemblages, and whether these changes can be linked to declining populations I will address this research gap in *Chapter 5*.

1.4.4 Transient species

Another theory explaining the apparent excess of rare species within assemblages that are monitored over time is the core-transient hypothesis (Magurran and Henderson, 2003). This theory explains the excess of rare species within assemblages by attributing a large proportion of rare species to being transient visitors, and not members of the "core" assemblages that underpin functioning of the system. This theory is closely related to the core-satellite species hypothesis, where species are separated into "core" species that are generally abundant and widespread within assemblages, and "satellite" species that are generally locally uncommon and not widespread (Hanski, 1982). Transient species can be detected using temporal dynamics, because core species will generally persist over time while transient species will not (Magurran and Henderson, 2003). Core and transient species can have quite different population dynamics and compositional drivers. For example, core and transient species can exhibit different shaped abundance distributions (Magurran and Henderson, 2003). The structure, body size and diversity of core species can be explained based on niche partitioning, whereas random dispersal better explains transient species presence (Ulrich and Zalewski, 2006; Umaña *et al*., 2017).

The presence of transient species within assemblages is very common across taxa (Taylor *et al*., 2018), so their influence on the distribution of rare species may be substantial. Because

transient species populations are more strongly affected by stochastic processes than mechanistic processes, it is difficult to predict how such rare species populations should change. However, because of their fundamentally transient nature, the presence of transient species can drive up estimates of temporal turnover (Taylor *et al*., 2018). If increasing numbers of transient species are entering assemblages and so driving up estimates of temporal turnover, they may also be driving up or sustaining species richness levels despite declines in core species richness. If the increasing turnover is mostly a product of changes in transient species then there should not be increasing turnover detectable amongst core species. I seek to address the question of whether the increases in turnover detected by Dornelas *et al*., (2014) could mostly be a consequence of increasing transient species through two separate analyses. In *Chapter 4*, I ask whether there is increasing turnover amongst the dominant species, because these species are important members of the core assemblage. In *Chapter 5*, I focus on changes amongst rare species, and assesses whether increased immigration of rare species is closely linked to increasing species richness. If increasing numbers of transient species is the main driver of a general increase in turnover then I expect no suggestion of increasing turnover of dominant species and increasing locally rare species immigrating into assemblages.

1.4.5 Biotic homogenisation

Immigrations, extinctions, and individual movements between locations can combine to increase the genetic, functional or taxonomic similarity of different sites (Olden *et al*., 2004). This process is called biotic homogenisation, and increasing biotic homogenisation may play an important role in the modern biodiversity crisis (Olden, 2006).

Genetic homogenisation happens when the genetic variety within a species is lost, or when different but similar species hybridise (Olden *et al*., 2004). The main mechanisms of genetic homogenisation are intentional translocations of populations by humans, genetic bottlenecks due to population declines, and the introduction of species outside their original ranges. The consequences of genetic homogenisation are poorly understood (Olden *et al*., 2004; Petsch, 2016), but this process has the potential to substantially affect ecosystem functioning and species adaption potential.

Functional homogenisation takes place when generalist species increasingly replace specialists species as a response to changing conditions (Clavel *et al*., 2011). Functional homogenisation can also take place if functionally similar species are introduced into systems

(Pool and Olden, 2012). This replacement of many functionally diverse species with a few functionally similar but successful species also leads to taxonomic homogenisation. Species that are well adapted to anthropogenically altered habitats, termed "winners", replace many local species, termed "losers" (Lockwood, 1999; Nee and May, 1997; Olden *et al*., 2004; Rooney *et al*., 2007).

Taxonomic homogenisation may take place because the species that are likely to be winners are also not distributed evenly among taxonomic groups, with families such as the grasses (*Poacae*) and the ducks (*Anatidae*) having more recorded successful invasions than would be expected from a random distribution (Mckinney and Lockwood, 1999; Pyšek, 1998). This could lead to a few species dominating globally, and these few species being closely related (Mckinney and Lockwood, 1999). In this way, taxonomic homogenisation can also cause phylogenetic homogenisation (Petsch, 2016).

Biotic homogenisation may be a consequence of shifting environmental conditions. For example, a substantial biotic homogenisation of marine fish assemblages was detected despite no change in species richness in North Atlantic groundfish assemblages, and this change was largely attributed to warming of the colder northern waters (Magurran *et al*., 2015). Species introductions can also cause biotic homogenisation. Invasive species caused taxonomic biotic homogenisation in grass layers of the Brazilian Cerrado, and the addition of these non-native species caused increasing species richness (Kortz and Magurran, 2019). Although Dornelas *et al*. (2014) detected no systematic loss of species richness at the assemblage level, they detected increasing turnover. This surprising result was partly attributed to the effects of biotic homogenisation, as species lost in local assemblages may be replaced with invaders. Although I do not directly test for evidence of biotic homogenisation in my thesis analyses, I include tests for increasing turnover and functional shifts of dominant species in *Chapter 4*, and I consider the balance of immigration and extinction events of rare species in *Chapter 5*. I will also discuss the implications of the results of my analyses in relation to biotic homogenisation in *Chapter 6*.

1.5 Aims of this thesis

In this thesis, I aim to address some of knowledge gaps outlined above. My overall aim for this thesis is to contribute to our knowledge and understanding of how assemblages change, and make informed suggestions on how to monitor change effectively. I focus on

assemblages rather than communities because this is the level at which most local ecological data above species-specific populations is collected.

Specifically, I ask four questions:

1. How influential is the sampling approach when estimating assemblage species richness and composition?

   There are substantial gaps in our understanding of biodiversity change, particularly in under-sampled tropical areas. Appropriate use of existing datasets, such as historical natural history collections and existing survey data, could help to efficiently and effectively decrease this knowledge gap. Before such data can be used for assessing temporal change, however, we need to know the biases introduced by different techniques when estimating assemblage species richness and species composition. I will address this issue in *Chapter 2*, where I compare estimates of freshwater fish assemblages using data gathered from a targeted two-year survey and historical museum collection records.

2. How closely do changes in the currencies of numerical abundance and biomass relate: do changes in one currency predict changes in the other currency?

   Although numerical abundance and biomass are sometimes used interchangeably (i.e. Taper and Marquet, 1996), they are not equivalent (Henderson and Magurran, 2010; Morlon *et al*., 2009). Understanding how changes in these two currencies relate is important for monitoring assemblage size, as well as elucidating potential shifts in body size and resource partitioning. This question of numerical abundance and biomass change is addressed in *Chapter 3*, where I undertake a meta-analysis across habitats and taxonomic groups to measure change in assemblage size, and specifically to test whether change in currency predicts change in the other. To provide further detail on the links between numerical abundance and biomass, I also assess how variable predation level are in Trinidadian freshwater fish assemblages, and how the currency choice influences these results.

3. Is there evidence for directional changes in the composition and structure of assemblages across systems?

To answer this question, I test a number of hypotheses regarding how different aspects of assemblages are changing (**Table 2**). Based on previous meta-analyses of assemblage change, I expect no systematic trends in species richness (Dornelas *et al*., 2014; Vellend *et al*., 2017, 2013) or assemblage size quantified in terms of numerical abundance (Dornelas *et al*., 2014; Gotelli *et al*., 2017). However, assemblage size in terms of biomass may be systematically decreasing if individuals are decreasing in body size as a reaction to increased disturbance. In addition to assessing how changes in numerical abundant and biomass relate, in *Chapter 3* I also test for systematic shifts in assemblage size measured in both currencies. According to theories relating to assemblage stability (Section 1.3.2 *The maintenance of assemblage functioning*) assemblages may still be experiencing substantial shifts in terms of species composition, dominance structure, and functioning, despite relatively stable assemblage size and species richness. Detecting such shifts can be challenging, particularly when assessing across a wide variety of systems. In *Chapter 4*, I focus on how the abundance and body size of dominant species are changing across different habitats and taxonomic groups, and ask whether there is increasing turnover in the identities of dominant species. In *Chapter 5*, I shift my focus to detecting changes in the number of rare species. In addition, I assess the relationship between changes in the number of rare species and changes in assemblage species richness, as well as exploring rates of immigration and extinction amongst rare species.

Table 2. The expected and trends in how different aspects of assemblage structure and composition are changing, based on the hypotheses I develop in each relevant chapter of my thesis.

	Currency	Chapter	Expected trend
Assemblage size	Numerical abundance	3	No change
	Biomass	3	Decrease
Dominance	Absolute	4	Increase
	Relative	4	Increase
Body size	Average length or weight of dominant	4	Decrease
Turnover	Turnover of dominant identity	4	Increase
Rarity	Number of singletons and doubletons	5	Decrease
Species Richness	Number of species	5	No change

4. What implications do my results have for understanding how biodiversity is changing at the local level?

In my final chapter, *Chapter 6*, I will discuss what my results mean for how assemblages are reacting to increased anthropogenic pressures. In addition. I will consider the implications for conservation and monitoring, as well as suggest further work to further elucidate structural and functional change within assemblages, as well as to increase our understanding of the mechanism of assemblage composition.

Chapter 2

How methods used to collect data shape conclusions about assemblage composition

Parts of this study will be published in the journal article:

Jones FAM, Rutherford M, Deacon AE & Magurran AE. (*Accepted*) Quantifying regional biodiversity in the tropics: a case study on freshwater fish in Trinidad and Tobago. Biotropica.

2.1 Abstract

There are substantial gaps in our understanding of biodiversity change, particularly at regional scales. This lack of understanding is especially severe in the tropics, where diversity is often high but data are sparse. Targeted surveys and historical museum collections are increasingly being used to meet the need for accurate information, but the extent to which these contrasting data sources support meaningful inferences about biodiversity change in regional assemblages remains unclear. Here I evaluated the performance of these alternative methods in estimating the richness and species composition of the freshwater fish assemblages of Trinidad and Tobago. I compared estimates of regional species richness derived from two different freshwater fish datasets: a targeted two-year survey of Trinidad and Tobago rivers, and a historical museum collection submitted to The University of the West Indies Zoology Museum. Species richness was estimated using extrapolated rarefaction, and assemblage composition was benchmarked against a literature review.

Both datasets provided comparable estimates of regional freshwater fish species richness. The highest richness estimates of the datasets were within 10% of each other (survey 50 and museum 46 species). In both cases the best estimate of species richness from the literature review (65) fell within the range estimates from the extrapolated rarefaction models. In addition, there was a large overlap (85%) in species identities in the survey and museum datasets. Species missing from the two datasets tended to be narrowly distributed, invasive or transient. My results suggest that regional richness estimates based on survey and museum data are comparable, but both methods leave a lot of uncertainty regarding the presence of difficult to detect species. Museum collection data are, consequently, a viable option for setting reliable baselines of assemblage species richness and species composition in a tropical system, thereby widening options for meaningful monitoring and evaluation of temporal trends.

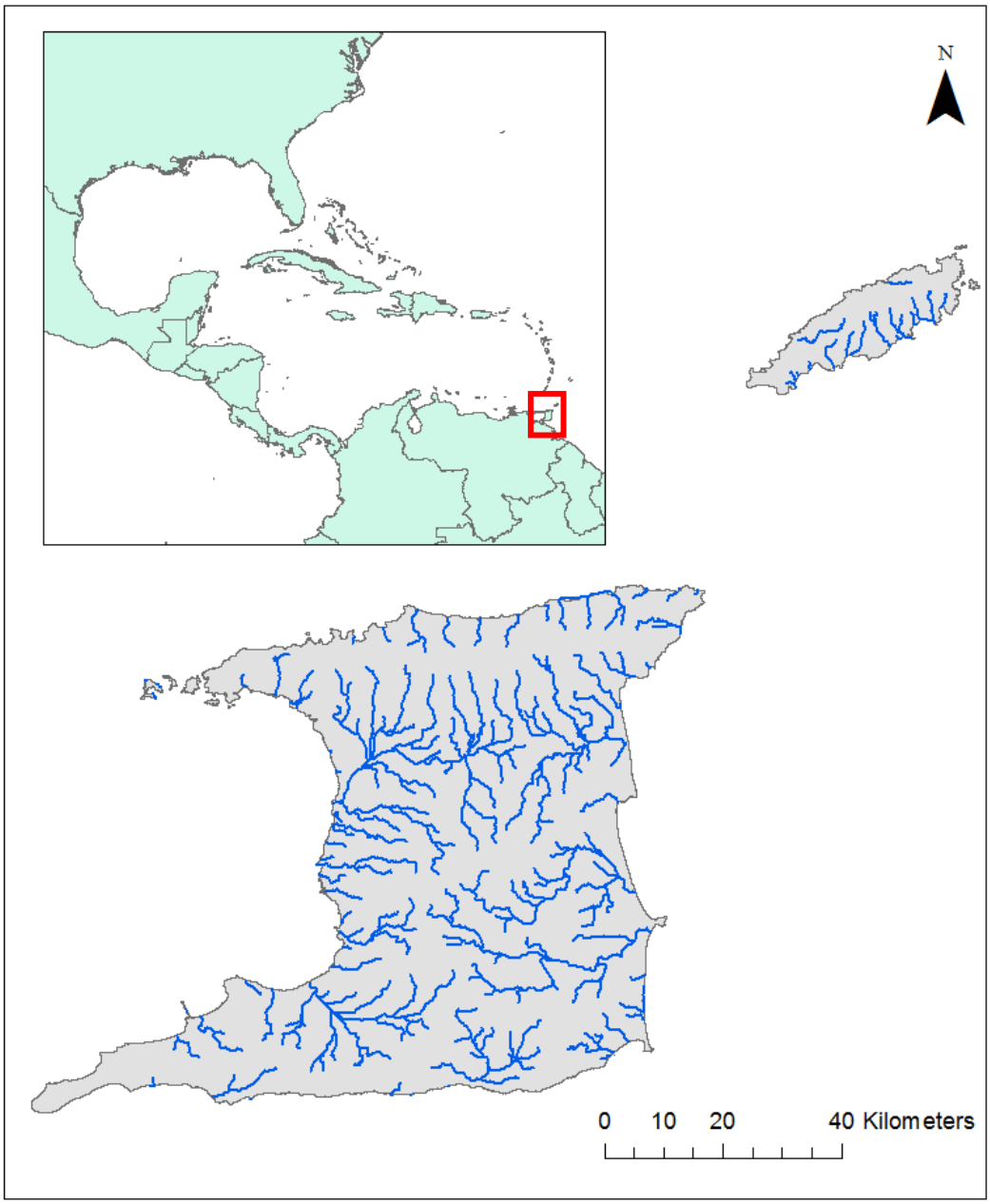


Figure 9. A map of Trinidad and Tobago. The river system that the freshwater fish species focused on in this chapter is displayed as blue lines. Inserted map shows the location of Trinidad and Tobago in relation to the Gulf of Mexico and South America. Trinidad and Tobago shapefile data © www.gadm.org. World data from R package mapdata. Rivers layer © Detlev Neumann.

2.2 Introduction

Although there is general agreement that we have entered the Anthropocene, an era likely to be characterised by mass extinctions (Barnosky *et al*., 2011; Dirzo and Raven, 2003), there are substantial gaps in our understanding of biodiversity change, particularly at regional scales. Many assemblages, notably those in the tropics, are poorly characterised (Collen *et al*., 2008). Even in well sampled areas, many species are very rare and are recorded in surveys only as singletons (Longino *et al*., 2002). The presence of the singletons, which have local abundances of 1, in species accumulation curves is a strong indicator that there are unseen species are yet to be detected (Chao, 1984). One solution to this problem of estimating species richness is to use statistical estimation approaches to deduce the number of unseen species in survey data (i.e. Chao & Jost, 2012; Gotelli & Colwell, 2001; Gotelli & Colwell, 2011).

The lack of information in often threatened tropical regions hinders effective conservation and policy decisions. Filling the information deficit is proving problematic because thorough local inventories and sampling (e.g. Bouchet *et al*. 2002; Longino *et al*. 2002) require extremely high levels of expertise and investment which are often unavailable in tropical regions. Even in relatively well sampled sites, a short period of sampling activity does not often come close to recording the actual number of species in an area (Fattorini, 2013). Difficulties in estimating species richness are exacerbated at regional spatial scales, where large areas of land may not have been surveyed. However, knowledge of species richness at this spatial scale is of fundamental importance for informing conservation initiatives, targeting information gaps, understanding global biodiversity patterns and providing baselines for further monitoring. This difficulty, coupled with the limited resources available for conservation, means that finding alternative ways of filling the tropical biodiversity knowledge gap is essential for supporting efficient conservation.

Historical natural history museum records and herbarium collections are potential alternative sources of data for biodiversity estimation, and are increasingly used to address ecological and conservation-based questions (Pyke and Ehrlich, 2010; Reznick *et al*., 1994). There are, though, concerns about potential biases in this type of data. The extent to which these different data sources provide meaningful inferences about biodiversity change in regional assemblages remains unclear. Survey data may underestimate species richness to a greater extent than museum records because sampling is generally targeted at specific areas or habitats, or depends on methods which may incompletely record certain taxa (Guralnick

and Van Cleve, 2005). However, while museums typically seek to maximise the range of specimens in the collection, they rarely set out to enumerate the species that co-occur in functioning ecosystems. Sampling for museums is generally *ad hoc* and undertaken by a variety of uncoordinated collectors. This leads to sampling aggregating around accessible areas or centres of population (Engemann *et al*., 2015; Guralnick and Van Cleve, 2005; Soberón *et al*., 2000; Tobler *et al*., 2007). Another bias is the "rare representation" effect: the tendency for collectors to favour rare species combined with longer collection times, which gives a greater likelihood of finding species outside of their normal ranges (Guralnick and Van Cleve, 2005; Pyke and Ehrlich, 2010). The rare representation effect may cause overestimation of species richness, which in turn might inflate the importance of transient species who do not contribute to ecosystem processes. These biases may be intensified in tropical regions where there were historically fewer collectors, and less resources available. Comprehensive species lists are therefore accumulated over time, and often include transient taxa and misidentifications, so such lists are not necessarily an informative guide to the species actually present in an assemblage during a defined time period (Phillip *et al*., 2013). Understanding biases inherent in museum data is crucial for effectively utilising this potential data source (Newbold, 2010). There is consequently a need for a better understanding of how well museum data perform in estimating regional biodiversity in the more diverse but less well sampled tropical regions.

Previous assessments of the relative utility of biodiversity quantifications from survey data and museum collections have focused on species richness rather than species identities (Guralnick and Van Cleve, 2005; Pyke and Ehrlich, 2010). However, biodiversity change can be significantly decoupled from species richness change when there is extensive turnover within assemblages (Dornelas *et al*., 2014; Hillebrand *et al*., 2017; Vellend *et al*., 2017, 2013). Accurate assessment of turnover (beta diversity), both spatial and temporal, is becoming increasingly important to understanding biodiversity change (Dornelas *et al*., 2014; McGill *et al*., 2015). There is consequently a need to understand uncertainties and biases not only of species richness estimates, but also of species identities recorded within these contrasting datatypes. For example, previous research suggests museum records may provide useful estimates of species richness, but that species identities may be biased towards rare species (Guralnick and Van Cleve, 2005; Pyke and Ehrlich, 2010). This is concerning, especially if species lists from one method will be used as baselines for further assessments using data collected from other methods.

To elucidate the comparability of different data collections, I assess the relative utility of targeted surveys and museum collections in estimating the biodiversity of freshwater fish in Trinidad and Tobago. First, I evaluate the performance of these alternative data sources when estimating the species richness of the freshwater fish fauna and benchmark my results against a recent literature review. Secondly, I analyse the identities of the species recorded by both methods to assess which species are absent, and to pinpoint possible biases in types of species detected.

My initial expectations regarding biases in the datasets are as follows:

1. The museum data will contain more transient species than the survey data because the longer period of time the museum dataset covers allows for a greater chance of finding a species that subsequently becomes locally extinct.

2. There will be more species with specialized habitat requirements or narrow spatial distributions in the museum collection data than the sampling data. I expect this because of biases associated with museum collection data, specifically the "rare representation effect" where collectors target rare species (Guralnick and Van Cleve, 2005; Pyke and Ehrlich, 2010).

3. Most species missing from both datasets will be those that are narrowly distributed or habitat specialists, because these uncommon species are least likely to be noticed by collectors or sampled by systematic surveys.

2.2 Methods

2.2.1 Study area

The country of Trinidad and Tobago is formed of two main islands lying to the northeast of Venezuela. Trinidad, the larger island, is 4820 km^2, and is only 11.3 km from Venezuela. Tobago is far smaller at 308 km^2 and sits 30.6 km from the coast of Venezuela. The climate of both islands is tropical, with temperatures typically ranging from 17°C to 33°C. The islands support a variety of freshwater habitats. Streams in the north of Trinidad and in Tobago contain mostly clear, fast flowing water with hard substrata ranging from boulders to gravel. The more southern parts of Trinidad contain slower, more turbid streams, with substrata ranging from sand to mud.

2.2.2 Data sources

The systematic survey data were collected by Dr Dawn Phillip as part of her PhD thesis (Phillip, 1998). Sampling was designed to provide useful data for the conservation and management of the freshwater fish of Trinidad and Tobago. Ninety-one stream and river sites across Trinidad and Tobago were selected, representing all major drainages, biogeographic regions and river types. Each river had between one and three sampling locations. Sampling took place over two years (1997-1998), and 22 sites were sampled twice. Consistent sampling methods were used throughout, with small adjustments depending on stream type. Wherever possible, seine nets were used to block off sections of around 50m of river. Then either electrofishing in clear water, seine netting in turbid water, gill and trammel nets in larger rivers, or a mix of methods, were used to catch as many fish as possible in the blocked off sections. Species and abundances at each site were recorded before fish were returned to the stream at the point of capture.

The University of the West Indies Zoology Museum (UWIZM) is the *de facto* zoological collection for Trinidad & Tobago, and one of the largest collections in the Caribbean. At the time of writing there are an estimated 70,000 specimens in the collections, the majority of which are local in origin. Although there was sporadic collecting of freshwater fish species from as early as 1936, the first significant fish collecting began in the mid-1960s and persisted through the rest of the 20th century. Few additions were made in the 2000s but from 2010 onwards there were significant additions from work done by visiting researchers.

For my analysis, I use collection year as the collection unit of the museum data (Petersen and Meier, 2003). The nomenclature of the freshwater fish species in both the survey and the museum collection was also checked using the list of old and new species names provided by a key of Trinidadian fish species (Phillip *et al*., 2013), ensuring that all names used in the final analysis were up to date and comparable.

2.2.3 Analysis

Freshwater fish species lists, particularly those for islands, typically include fish species that are mostly restricted to freshwater systems, fish species that are normally found in estuaries, and fish species that are predominately marine but occasionally move upstream. In addition, these lists will include anadromous and catadromous species. For this analysis I decided to adhere to Phillip *et al*. (2013)'s definition of freshwater fish, based on habitat preference and taxonomy. I used this recent literature review (Phillip *et al*., 2013), that includes a

comprehensive species list and key of fish species, to identify these freshwater fish. I selected from this list only species that are considered by Phillip *et al*. (2013) as truly freshwater, not those that are usually considered to be marine or coastal species. I included transient species but not species that Phillip *et al*. (2013) considered misidentifications. Dr Phillip also submitted specimens and records to the museum between 1997 and 1998 as part of her survey. To avoid any influence of these records on the museum collection data results, I removed all samples collected by Dr Phillip in 1997 and 1998.

I used rarefaction and extrapolation curves using the 'iNEXT' R package (Chao *et al*., 2014) to estimate freshwater fish species richness in Trinidad and Tobago. Extrapolated rarefaction enables the user to estimate the number of species that would be detected if sampling was increased to include an additional number of individuals or sampling units. Individuals should be sampled at random (Colwell *et al*., 2012), an expectation that museum data (and most ecological surveys) will not satisfy. Nonetheless, extrapolated rarefaction is a robust and informative method with different types of data, e.g. phylogenetic diversity (Chao *et al*., 2015; Hsieh, Ma, & Chao, 2016b) and distributions of stone tools in Pleistocene North America (Buchanan *et al*., 2017). For both datasets, I used the "incidence_freq" datatype option, which applied sample-based rarefaction rather than individual-based rarefaction. For the Museum data, I used year the year an acquisition was recorded as its sample ID. I chose sample-based rarefaction rather than individual-based rarefaction because the sampling units in sample-based rarefaction are representative of the sampling area, which is a less stringent assumption than for individual-based rarefaction (R.K. Colwell, *pers coms*). I then benchmarked the estimated species richness numbers against the species richness estimate provided by a comprehensive species list collated using all available fish records and expert knowledge of the Trinidad and Tobago freshwater fish (Phillip *et al*., 2013)

To explore the effects of including effort in the museum data species richness estimate, I fitted a Michaelis-Menten (MM) accumulation curve using the R package *drcR* (Ritz, Baty, Streibig, & Gerhard, 2015). Because sampling effort was kept uniform for the field survey data, I only fitted the MM curve to the museum data. Cumulative effort was calculated as the accumulating number of freshwater fish acquisitions submitted to The UWI Zoology Museum.

To further understand whether the survey dataset and the museum collection dataset differ in the types of fish they represent, I categorized each fish species by status (i.e. native/non-

native), by habitat specificity, and by how widely it was distributed across Trinidad and Tobago using information in Phillip *et al*. (2013) and FishBase (fishbase.org) - see **Table 3** and **Appendix Table 1**. I compared the characteristics of the species observed in the survey and museum data against the results of a null model. The assumption of the null model is that each species has equal probability of being recorded if it is (or has been) found in the rivers of Trinidad and Tobago. For each iteration of the null model, 39 species were randomly selected from the list of 66 species that are likely to be present in Trinidad and Tobago according to Phillip *et al*. (2013). I chose 39 because this is the maximum number of species observed in either dataset. I recorded the native status, distribution, and habitat specificity of each of the randomly selected species, and then proceeded with the next iteration. The model included 1000 iterations. I then calculated the quantiles of the observed numbers of fish in the survey and museum data for each category in relation to the null model results. Quantile values of less than 0.025 or more than 0.975 fell outside the 95% range of the null distribution, and consequently were considered significantly different from the null expectation.

Table 3. Category descriptions for assigning species characteristics. Information was extracted from (Phillip *et al*., 2013). Any fish described as "mistake" were removed from the analysis during data preparation.

Designation	Description
Status	
No data	No data on this characteristic in the fish key
Introduced	Species colonised from a human introduction
Mistake	Misidentifications
Presumed native	Presumed native to Trinidad and Tobago
Recent Colonist	Natural colonists from the Orinoco River
Transient	Species not recorded in the last 2 to 3 surveys. They are natural colonists from the Orinoco River that did not become established
Habitat Specificity	
No data	No data on this characteristic in the fish key
Specialist	Lives in only one water type, e.g.. clear and fast flowing
Generalist	Can live in different water types, i.e. clear fast flowing water and turbid water
Distribution	
No data	No data on this characteristic in the fish key
Narrow	Only found in a few sites
Intermediate	Either found in a subsection of Trinidad and Tobago that is more than a few streams or fish described as "widely distributed" in a subsection of Trinidad and Tobago
Wide	Found in most of Trinidad and Tobago, or found in both Trinidad and Tobago, or described as "widely distributed"

2.3 Results

2.3.1 Estimated species richness

The observed species richness curve of the survey data follows a smooth accumulation curve (**Figure 10A**), visually suggesting an asymptote is close - an impression supported by the smoothed species richness accumulation curve (**Figure 10E**). Although there are far more records overall in the survey data than the museum data (**Table 4**) most species are found only at a few sites (under 20) (**Figure 10C)**.

In contrast to the survey data results, the museum data accumulation curve does not suggest an asymptote close to the 39 species recorded (**Figure 10B**). The smoothed species richness accumulation curve in **Figure 10F** also suggests the dataset is further from an asymptote than the survey data. Collection effort is extremely variable in the museum data, with over 200 records submitted in the 1990s and fewer than 100 for most other decades (**Figure 10D**). Variable collection effort strongly influenced the collection curve; when accumulated species richness is plotted against effort (measured as number of freshwater fish acquisitions) a smooth accumulation curve close to an asymptote is evident (**Figure 11**). There is, however, no noticeable increase in new species during the period of increased specimen submissions (**Figure 10B**).

Table 4. A breakdown of the numbers of acquisition records singletons (species only recorded once), doubletons (species recorded twice), and the observed number of species in the sampling and museum freshwater fish, as well as the number of freshwater fish estimated to be extant in Trinidad and Tobago according to rarefaction and extrapolation using iNEXT. The upper and lower bound are the 95% lower and upper confidence limits around the species richness estimates.

Dataset type	Acquisitions	Sampling Units	Singletons	Doubletons	Species Observed	Species Richness estimate	Lower bound	Upper bound
Survey	21153	114	4	3	38	50 (+/- 17)	40	131
Museum	785	30	2	3	39	46(+/- 6)	40	68

Table 5. A breakdown of the status, distribution and habitat preference characteristics of all freshwater fish species in Trinidad and Tobago as stated in the literature review by Phillip *et al* (2013). A further breakdown of the characteristics of the fish found in the Survey and Museum datasets is also included, and the quantiles of these values in relation to the null model results. Quartiles falling outwith the range of 0.025 - 0.925 lie outside the 95% range of the null distribution. Finally, I include a breakdown of the characteristics of the fish found in either the Survey or the Museum data.

		All Species	Survey	Museum	Survey Quantile	Museum Quantile	Not found
Status	No data	3	0	0	0.18	0.18	3
	Introduced	5	2	2	0.42	0.42	3
	Native	53	33	34	1.00	1.00	16
	Recent Colonist	4	3	3	0.92	0.92	0
Distribution	No data	11	0	0	0.00	0.00	11
	Narrow	13	6	4	0.34	0.05	6
	Intermediate	24	19	22	1.00	1.00	2
	Wide	17	13	13	0.99	0.99	3
Habitat	No data	2	0	0	0.00	0.00	2
	Specialist	23	14	14	0.84	0.84	7
	Generalist	40	24	25	0.94	1.00	13

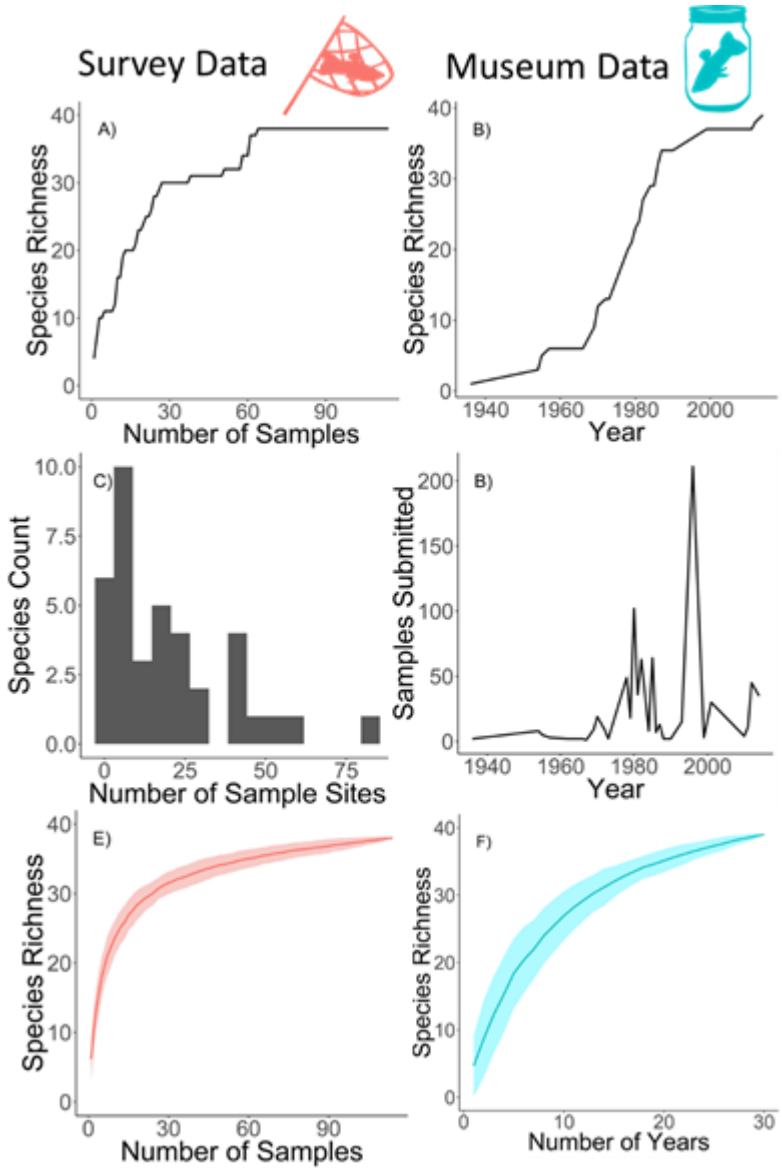


Figure 10. Plots of the Trinidad and Tobago freshwater fish targeted survey data and museum collection data. Plot (A) is the accumulation of species richness as new sites are added to the survey data in terms of the actual temporal sequence of data collection. Plot (B) shows the accumulation of species richness in the museum collections through time. Plot (C) shows the frequency of species found in multiple sites, and plot (D) shows the unequal distribution of sample submissions to the museum collection over time. Plots (E) and (F) show the smoothed accumulation curves for the survey and museum data, respectively. These plots display the mean and standard deviation of species richness accumulation over samples or years calculated using 100 random permutations of the data.

The rarefied extrapolation estimations were within 10% of each other (50 species for the survey data, 46 for the museum data), and they both lie well within each other's upper and lower bounds (**Table 4**). The survey data had higher uncertainty around this estimate, with the upper 95% species richness estimated as 130 species as opposed to the 68 estimated from the museum data. The range of estimates predicted by both data types included the value (species richness =65) reported by the comprehensive key and species list (Phillip *et al.*, 2013). Note the S=66 species richness value quoted in the text of Phillip *et al*. 2013 (p.7) is a miscount of the true number listed in the table of species. The number of sampling units in both datasets varied substantially (114 for the survey, 30 for the museum data; **Figure 12A**), but both datasets achieve high proportions of coverage of the data (**Figure 12B**).

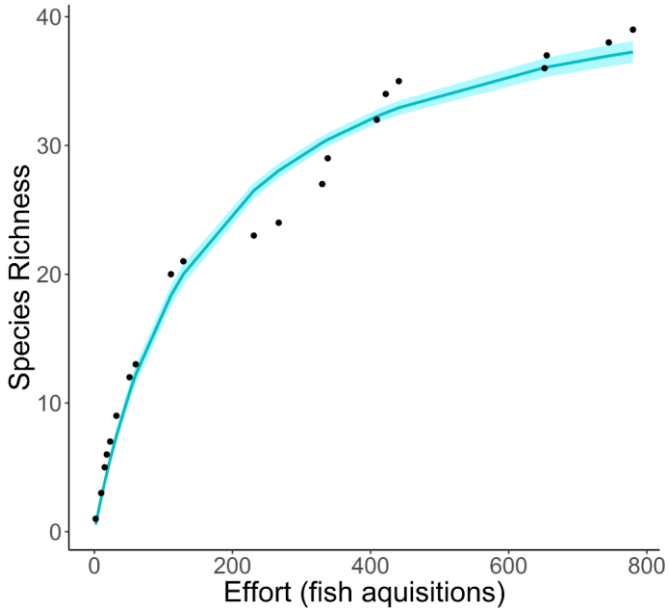


Figure 11. Michaelis-Menten (MM) curve fitted to the Trinidad and Tobago freshwater fish museum data to estimate regional species richness. Cumulative effort is defined as the accumulating number of freshwater fish acquisitions submitted to the museum. The asymptote was estimated using this model as 44 (+/- 1.9) species. The ribbon around the model estimate represents the standard error around the model prediction,

Using effort instead of year did not improve species estimates for the museum data. A parametric Michaelis-Menten model using accumulated effort in terms of number of freshwater fish acquisitions estimated regional species richness as 44 +/- 1.9 species (**Figure 11).**

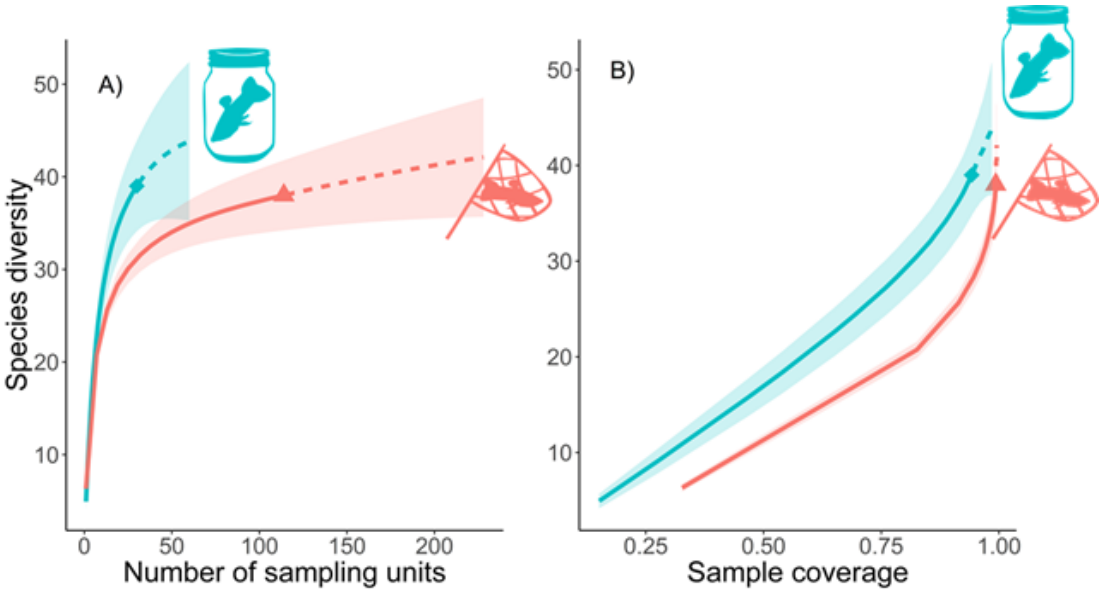


Figure 12. The sample based (A) and coverage based (B) rarefaction curves for estimating numbers of freshwater fish in Trinidad and Tobago using the survey data (red triangle) and the museum data (blue diamond).The dashed part of the curve represents the extrapolated species richness, and the ribbon around the line is the 95% confidence intervals. Despite the far greater number of samples in the survey data than the museum data, both data types display coverage of close to 100% and converging species richness estimates.

2.3.2 Assemblage composition

There were fewer species missing from the museum data but recorded in the survey data (4) than recorded in the survey but missing from the museum data (6) (**Figure 13**). No transient species were recorded in either dataset (**Table 5**), and most species in both datasets were native. A high proportion of species missed by both data collection methods either were lacking in data, transient, narrowly distributed or habitat specialists (**Table 5**).

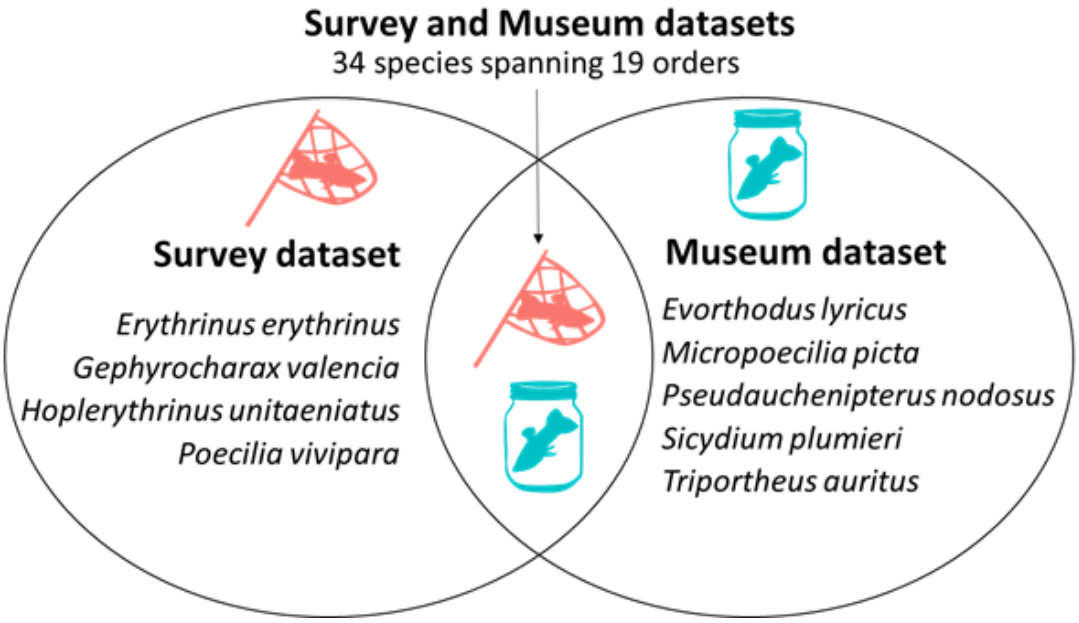


Figure 13. A breakdown of which species were recorded only in the survey data and only in the museum data. The majority (34) species were recorded in both datasets. For a complete list of which species where found in each dataset see **Appendix Table 1**.

Contrary to my expectation, there were no biases evident between types of fish recorded in the survey and museum data (**Table 5**; **Figure 14**). Although the range of estimates of species richness for both data types included the best estimate from Phillip *et al*. (2013)'s literature review, the fraction of native species was higher in both cases than in the overall list provided by Phillip *et al*. (2013). Both datasets also included more intermediately or widely distributed species than this overall list, although the difference was more marked in the museum data than the survey data. There are also more habitat generalists in the observed data (both methods) than expected if they were a random draw from the overall list. This difference, however, is less pronounced because the number of habitat generalists in both surveys fall within the 95% quantiles of the null model.

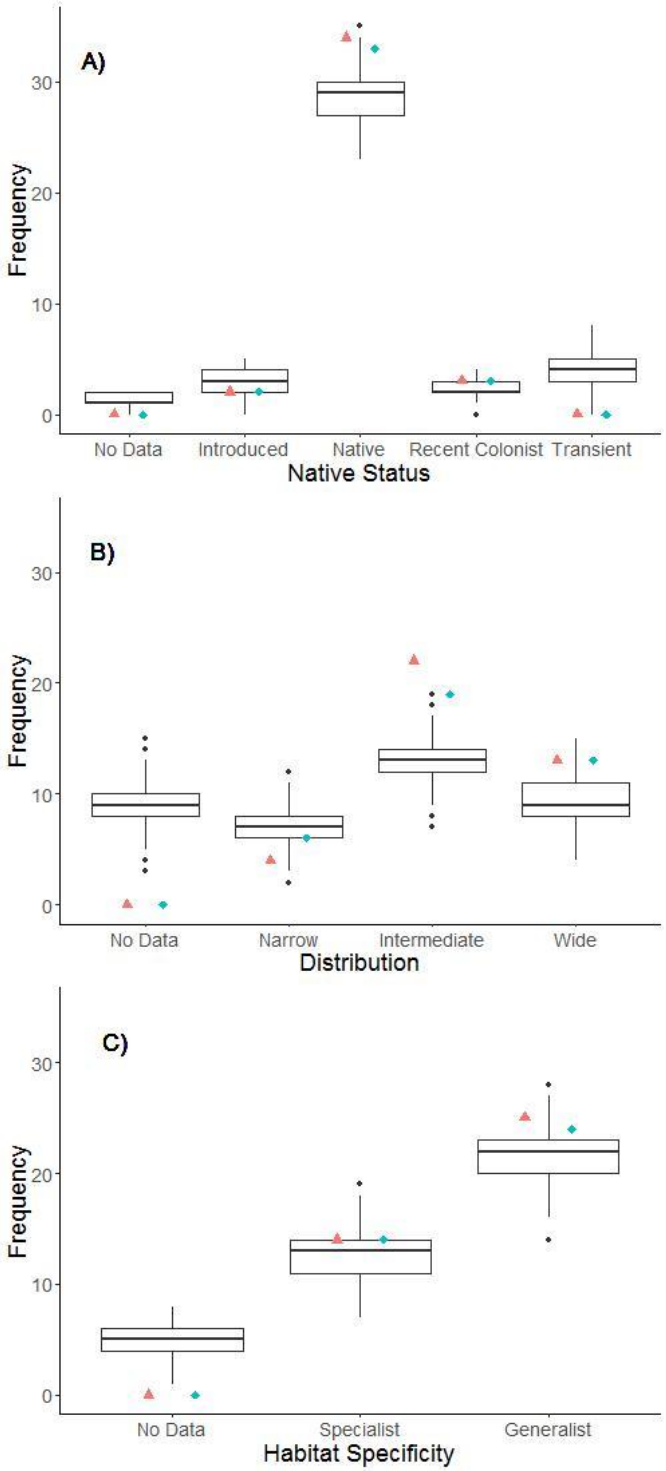


Figure 14. The native status (A), distribution (B) and habitat specificity (C) of 39 fish randomly selected by a null model with 1000 iterations (black boxplots), compared to the observed habitat specificity of species found in the survey data (red triangles) and museum data (blue diamonds). Box plots show medians, upper and lower quantiles and outliers.

2.3 Discussion

Despite the two orders of magnitude fewer records contained in the museum data than the targeted survey data, both datasets provided comparable estimates of regional freshwater fish species richness in Trinidad and Tobago. The species richness estimates of the museum and survey data were within 10% of each other (50 species and 46 species, respectively), and there was a large overlap (85%) of species identified. Both estimates fall 20% below the maximum number (65) of species potentially present according to the exhaustive list (Phillip *et al*., 2013; **Table 4**), but the 95% confidence intervals around the estimates are inclusive of the maximum number of potential species. Both coverage-based rarefaction curves (**Figure 12B**) ended close to the 100% coverage mark.

I expected differences in the composition of species observed in the two contrasting datasets because of biases in the collection methods of the museum data. For example, sampling for historical museum collections generally occurs *ad hoc* by a variety of uncoordinated collectors typically leading to an overrepresentation of easily accessible areas and centres of population (Engemann *et al*., 2015; Guralnick and Van Cleve, 2005; Soberón *et al*., 2000; Tobler *et al*., 2007). In addition, the rare representation effect could cause overestimations of species richness, which in turn might inflate the importance of transient species that do not contribute to ecosystem processes. Contrary to my expectations, I found a striking similarity between the identities of the species recorded in the survey and museum data, suggesting these biases do not strongly influence regional species richness estimates. The majority (85%) of species were recorded in both datasets. In addition, there was no indication of biases in types of species recorded; the museum collection data did not contain more transient species, habitat specialists or narrowly distributed species, than the survey data.

My results suggest that, although collection methods differ considerably between datasets, survey and museum data provide comparable estimates of the regional assemblage species composition. Consequently, historical museum collection data are potentially useful for analysing other aspects of biodiversity change in addition to species richness. Rates of turnover of species identity within assemblages, for instance, could be assessed with species lists. In this case, museum data could also be used to set baseline assemblage species lists to compare contemporary assemblage data. Turnover rates are variable and driven by a complex collection of biotic and abiotic factors (Korhonen *et al*., 2010), and warrant more analysis. Datasets such as the collections held at The University of the West Indies Zoology

Museum, Trinidad, could serve as a baseline for furthering our understanding of turnover within communities.

Systematic surveys provide robust data on species distributions and abundance, but they are not practical in many cases because undertaking such surveys can be expensive and requires good access to expertise and sites. The survey I used in this analysis took place over two years and involved many person-hours of preparation and field work. Even in relatively well sampled sites, a short period of sampling activity does not often come close to the actual number of species in an area (Fattorini, 2013). This is particularly a problem in tropical regions, where there is a substantial need for data. Alternative data gathering exercises, namely intensive local sampling areas (i.e. Bouchet, Lozouet, Maestrati, & Heros, 2002; Brown *et al*., 2018; Longino *et al*., 2002) could also be useful, but these sampling endeavours also require extremely high levels of expertise and investment which are often unavailable, and are not practical on a regional scale. In these cases, museum and other historical natural history collections provide useful resource for estimating regional species richness. This is not to say that historical museum data can or should replace systematic survey data in all cases. For instance, an aspect of biodiversity change which may strongly affect ecosystem functioning is reordering of species abundances with assemblages (Jones *et al*., 2017). To what extent such reordering of assemblage structure, in particularly whether dominant species are changing identity, requires representative relative abundance data which cannot be extracted from *ad hoc* museum collections (Garcillán and Ezcurra, 2011).

While both datasets investigated in this chapter gave similar estimates of species richness and assemblage composition, there was divergence between their estimates and that of a recent literature review and key (Phillip *et al*., 2013; **Table 3**). Both data types underestimated the species richness of the freshwater fish assemblage, although the 65 species predicted by the literature review falls within the uncertainty around the estimates. The species missed from the studies were not random in characteristics; they tended to be narrowly distributed, habitat specialists or recent additions to the Trinidad and Tobago freshwater fauna. Such biases are extremely common in ecological assemblage data (Longino *et al*., 2002), with most undescribed species believed to be narrowly distributed and uncommon within their home ranges (Pimm *et al*., 2014). These biases raise the question of whether both my empirical datasets underestimate species richness or whether the exhaustive list compiled from a literature search is an overestimate. This is an important

consideration, because how much emphasis is given to the most difficult-to-detect species in an assemblage heavily influences extinction and turnover rates. Recently detected species may go extinct just after their discovery, or species may go extinct before discovery (Barnosky *et al*., 2011; Lees and Pimm, 2015). This is particularly likely if they are transient species (Magurran and Henderson, 2003) or have restricted distributions (Pimm *et al*., 2014).

A difficulty when assessing the effectiveness of museum collections in estimating regional species richness is how to delimit the assemblage of interest. Despite having the benefit of a recent review of freshwater fish in the rivers of Trinidad and Tobago (Phillip *et al*., 2013), I was left with some ambiguity as to how to tackle this issue. In line with Phillip *et al*. (2013)'s suggestion, I did not include fish that are primarily coastal or marine species. However, these species still form part of the ecological community of lower reaches of some rivers. Another difficulty was whether to include transient species in the "true" number of freshwater fish in the region. Phillip *et al*. (2013) do not consider the 8 transient species listed in their guide as true freshwater fish of the region, as they have not established in Trinidad and Tobago and are therefore unlikely to be found there in the present day. The long time periods over which data are collected, combined with the rare representation effect biasing acquisitions towards collecting novelties, means museum data are more likely to contain transient species than survey data (Guralnick and Van Cleve, 2005; Pyke and Ehrlich, 2010). How transient species are dealt with needs particularly careful deliberation when species richness is estimated from museum collection data. However, my analysis suggests this may not be a substantial problem, as there were no transient species acquisitions in the museum data. Transient species may be present in other museum datasets, but my analysis suggest that in this case at least, museum data are not sufficiently biased towards such species that they inflate regional species lists. It is worth noting, however, that transient species may have a stronger presence in smaller scales or in more mobile taxa. There is limited opportunity for freshwater fish to reach new locations, as they must follow the river system. The lack of mobility of freshwater fish is an issue for species immigrating to Trinidad and Tobago because this region is an island surrounded by saltwater. There is the possibility of fish from mainland South America reaching Trinidad and Tobago from the Orinoco River delta (Phillip *et al*., 2013), but colonisation is less likely for such movement limited species than for more mobile taxa such as birds or marine fish.

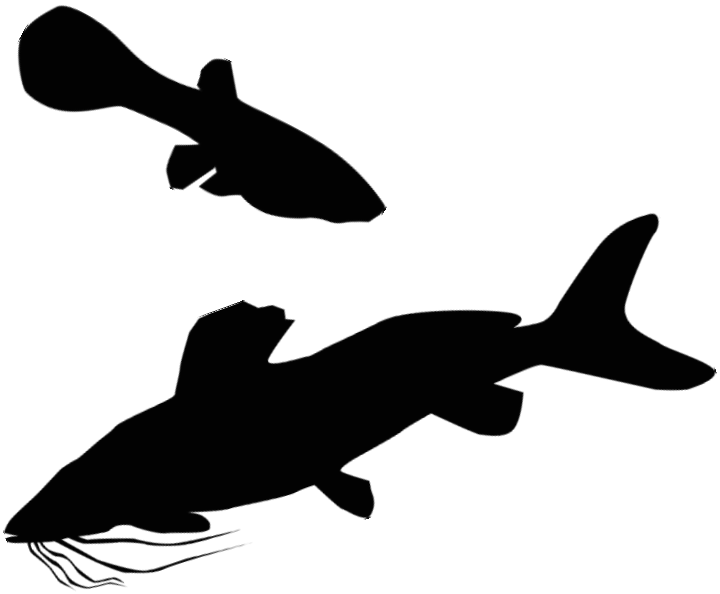
2.3.1 Concluding remarks

Uncertainty around biodiversity levels and distributions hinders our understanding of key biodiversity statistics and consequently our ability to make informed conservation decisions (Pimm *et al.*, 2014). Understanding the information gaps around biodiversity knowledge is essential for progression of the field (Hortal *et al.*, 2015). In my analysis, I demonstrated that both historical survey data and historical museum collection data can provide useful regional species richness estimates to use as baselines for assessing biodiversity change. Both datasets also provided comparable estimates of the identities of species within the assemblage, meaning species lists for assessing species turnover could be compiled from historical museum collection data as well as systematic surveys.

I also demonstrated the challenges in quantifying the exact number and identity of all species in an assemblage. There will almost always be some uncertainty regarding the presence or absence of difficult-to-detect species. Different methodologies may favour different difficult-to-detect species. There are consequently very few situations where an exhaustive species list it obtained using a single data collection method. This uncertainty means that species richness will always vary somewhat with the estimation method. The influence of this uncertainty regarding difficult-to-detect species needs special care when estimating regional species richness and undertaking turnover analyses. A failure to do so may cause underestimations of species richness and overestimations of turnover.

Chapter 3

The influence of numerical abundance and biomass in assessing biodiversity change



Parts of this study were published in the journal article:

Deacon AE, **Jones FAM**, & Magurran AE (2018). Gradients in predation risk in a tropical river system. *Current Zoology*, 64(2), 213 -221. http://doi.org/10.1093/cz/zoy004

3.1 Abstract

Assemblage size can be quantified in terms of numbers of individuals (numerical abundance) or biomass. The two currencies are sometimes used interchangeably, but although they are linked, they are not equivalent. Although the relationship between abundance currencies has been well studied, there is no consensus as to how these two currencies should co-vary over time. In particular, there is a lack of knowledge of how trends in numerical abundance and biomass relate. A better understanding of this issue will help elucidate the relationship between individuals and resource partitioning.

To address this issue, I undertook two complementary analyses. First, I ask how trends in assemblage size, measured in terms of numerical abundance and biomass, relate across habitats and locations. In line with other studies, I expected that numerical abundance would not be decreasing. For biomass, on the other hand, I expected a decreasing trend. My results for this analysis, however, suggests that neither numerical abundance nor biomass generally changing over time, although there is considerable variation around this general trend. When biomass did change, it largely tracked changes in numerical abundance. This result demonstrates little support for the prediction that smaller individuals are generally replacing larger individuals.

To examine how our understanding of the mechanisms that underpin assemblage structure is influenced by the choice of abundance currency, I then focused on a case study of guppy (*Poecilia reticulata*) predators in the rivers of the Northern Range, Trinidad. Both quantifications of predator abundance suggested a gradient rather than a dichotomy in high-low predation pressure, although the rankings of sites along this gradient were inconsistent between the currencies. These results show how inferences about the relative strength of different ecological mechanisms can be influenced by the currency used to measure abundance.

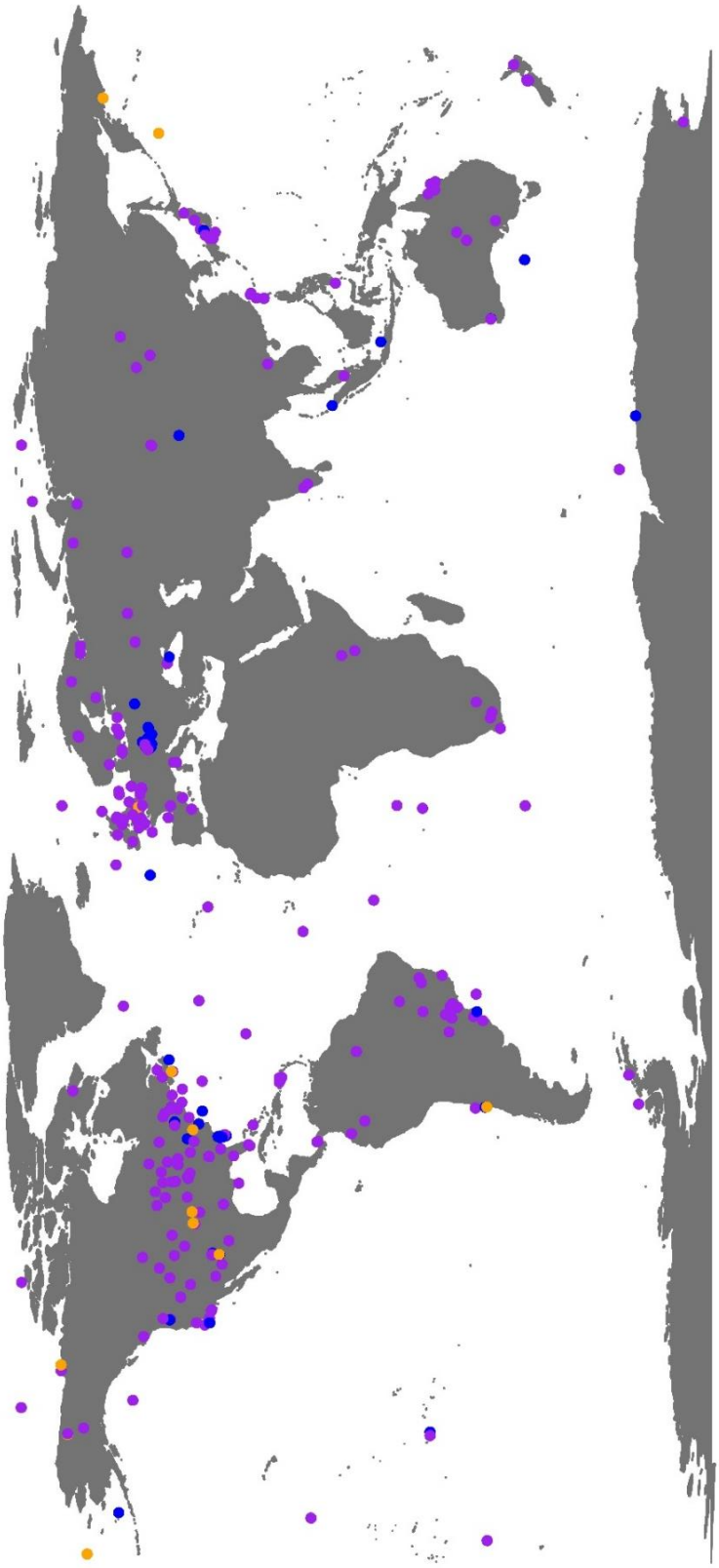


Figure 15. The distribution of assemblages used in the second analysis of Chapter 3. Points are the central locations of each assemblage, and colours represent whether assemblages contain assemblage size data recorded as numerical abundance (purple), biomass (orange), or both (blue).

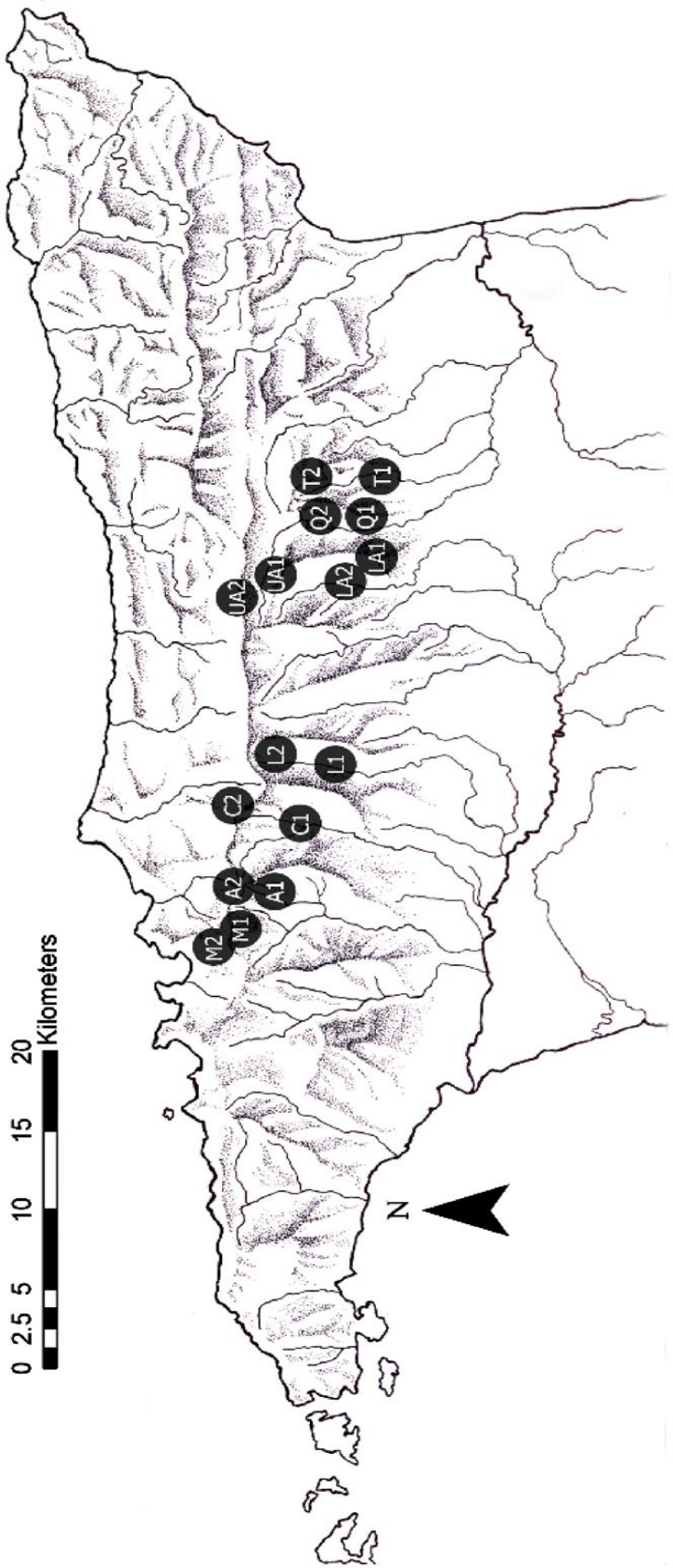


Figure 16. The location of the 16 sites across Trinidad's Northern Range. Site abbreviations are as follows: A1: Acono site 1; A2: Acono site 2; C1: Caura site 1; C2: Caura site 2; L1: Lopinot site 1; L2: Lopinot site 2; LA1: Lower Aripo site 1; LA2: Lower Aripo site 2; M1: Maracas site 1; M2: Maracas site 2; Q1: Quare site 1; Q2: Quare site 2; T1: Turure site 1; T2: Turure site 2; UA1: Upper Aripo site 1; UA2: Upper Aripo site 2.

3.2 Introduction

The size of assemblages, defined as how much life an assemblage is supporting at a given point in time (*Chapter 1*), can be quantified in terms of numbers of individuals (numerical abundance) or biomass. These two currencies are sometimes used interchangeably (i.e. Taper and Marquet, 1996), but although they are linked they are not equivalent (Magurran and Henderson, 2010; Morlon *et al*., 2009). Numerical abundance is more closely linked to assemblage dynamics, whereas biomass may be a better indicator of resource allocation (White *et al*., 2007). The relationship between biomass and numerical abundance has been well studied (e.g. White, Ernest and Thibault, 2004; White *et al.*, 2007; Dornelas, Phillip and Magurran, 2011; Ehnes *et al.*, 2014), but there is no consensus about how these two currencies should co-vary over time. Recognising how numerical abundance and biomass are linked over time is an important step in understanding assemblage composition, because the two currencies provide different insights into how species partition resources. In addition, a greater understanding of the relationship between currencies under increasing anthropogenic pressures will shed light on how assemblages are adapting to new conditions. This knowledge will be useful in predicting future scenarios and thus support conservation planning.

To gain a detailed understanding of the relationship between numerical abundance and biomass, I first focus my analysis on correlating how different currencies of assemblage size (numerical abundance and biomass) change over time across systems. A previous analysis of global assemblage size, using a subset of the assemblage data I use in this chapter, found no evidence for a trend in assemblage size measured in numerical abundance (Dornelas *et al*., 2014). There is, though, evidence for declining body size under increasing anthropogenic pressures (Daufresne *et al*., 2009; Duplisea and Castonguay, 2006; Petchey and Belgrano, 2010). A potential explanation for this decline in body size is that smaller species have generally more r-selected life strategies (Pianka, 1970), and so often live at higher densities. Smaller species can also be less vulnerable to local extinction due to higher reproductive output (Cardillo, 2003). It is worth noting, however, that body size is also intricately linked to niche space (Williams *et al*., 2010), and decreases in body size alongside increases in numerical abundance have empirically been noted due to shifts in niche space. For example, smaller mammal species were better adapted to increasingly shrub based habitats (White *et*

al., 2004). Not all decreases in body size will therefore directly lead to more r-selected life history traits.

There are various possible scenarios concerning change in numerical abundance and change in biomass over time. For example, in cases where smaller individuals replace larger individuals, there could be a noticeable decreases in the biomass of an assemblage despite no change in numerical abundance (**Figure 17A**). In an extreme case, where many small individuals replace a few large individuals, the currencies would negatively co-vary, meaning numerical abundance would increase while biomass decreased (**Figure 17B**). Conversely, trends in numerical abundance and biomass should positively co-vary if small individuals are not replacing larger individuals, because any change in numerical abundance would also influence biomass (**Figure 17C**). In this case, assuming there is no systematic change in numerical abundance, no systematic change in biomass would be expected. In this chapter, I intend to elucidate the relationship between numerical abundance change and biomass change by testing for evidence of any of these scenarios.

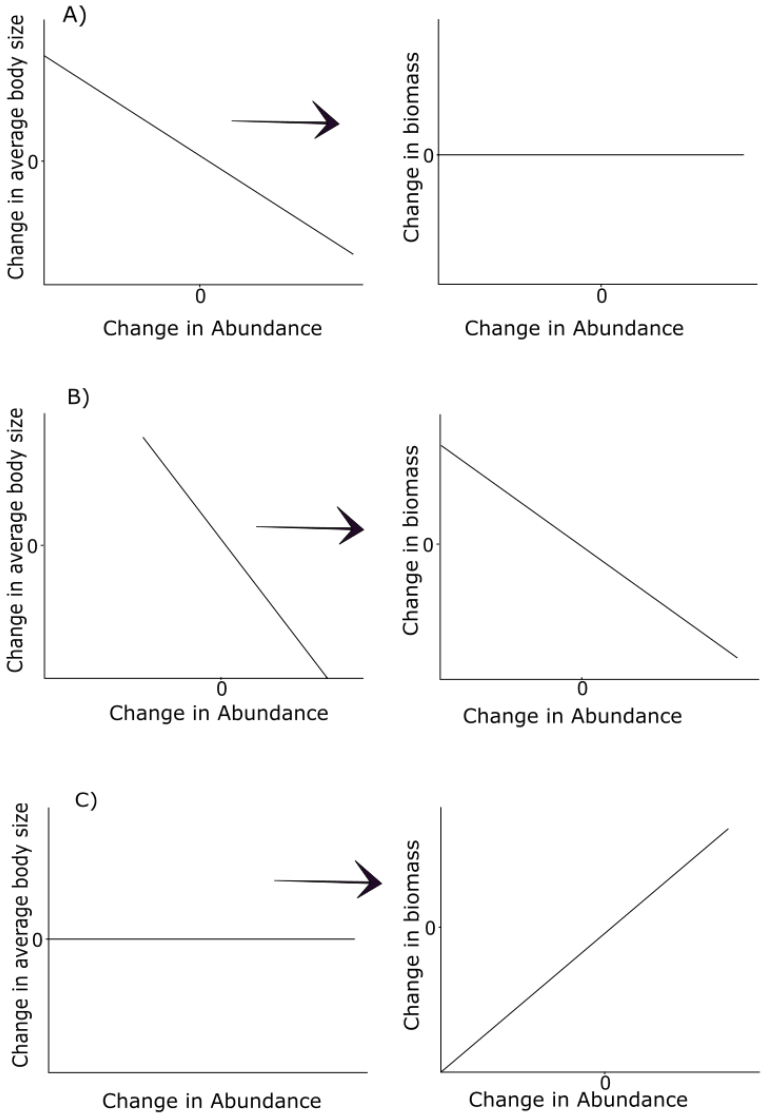


Figure 17. A conceptual diagram of how changes in average body size and assemblage size measured in numerical abundance interact, and how this relationship may influence the link between numerical abundance and biomass. Change in each case is the slope of change of the metric over time. In panel A), numerical abundance and body size negatively relate, meaning assemblages with increasing numerical abundance experience decreasing average body size. In this case, the changes in numerical abundance are balanced by changes in body size, so that biomass does not change alongside abundance. Panel B) shows an extreme example of a negative relationship between numerical abundance and average body size. In this case, shrinking body size is so pronounced with increasing abundance that the increase in numerical abundance does not balance decreasing body size, and so biomass decreases as numerical abundance increases. Alternatively, in panel C), body size does not change relationally to numerical abundance. In this case, biomass change positively co-varies with numerical abundance change, so that change in one currency of assemblage size predicts change in the other currency.

Following on from the global analysis of assemblage change, I then focus on a case study of an ecologically relevant ensemble (a guild within an assemblage, see *Chapter 1*) of guppy (*Poecilia reticulata*) predators in the rivers of Trinidad. The purpose of this case study is to explore how the choice of abundance currency can influence our perception of ecological questions. As an example, I aim to elucidate how the quantification and temporal dynamics of a highly influential mechanism that underpins assemblage structure, predation level (Jackson *et al*., 2011), differs between numerical abundance and biomass values. Understanding predation pressure in the freshwater rivers of Trinidad is particularly important because predation is the main source of selection in this system (O'Steen *et al*., 2002; Reznick and Endler, 1982).

The freshwater river communities in the Northern Range of Trinidad, where my study is based, provide a unique opportunity for assessing the effects of predator pressure on guppy population dynamics and evolution. Many of the streams in the Northern Range run parallel to each other and are interrupted by waterfalls which can be many meters high. These waterfalls provide natural barriers, preventing the upstream dispersal of certain fish species. Areas directly upstream of barrier sites are thus home to fewer species of guppy predator, and they are traditionally considered to be "low risk" sites for guppies. The sites downstream from the barriers tend to have more and larger predatory species, leading them to be considered "high risk" sites for guppies. This dichotomy between high and low risk sites, coupled with the individual variation between guppies, makes the Northern Range rivers a "natural laboratory" (Haskins *et al*., 1961), well suited for linking predation pressure to differences in a huge range of traits, including size, behaviour (Liley and Seghers, 1975), colouration (Endler, 1980) and numerous life history traits (Reznick and Endler, 1982). However, not all rivers have barrier waterfalls, and the extent to which the barriers limit the upstream movement of predatory fish varies.

Traditionally, guppy research has emphasized the contrast between the predation level extremes. However, the "low" and "high" risk categories have generally been based on presence or absence of species, either historically or at the time of sampling. This method of defining predation pressure has some potential issues. For example, sites are assumed to remain either high or low risk because the presence of waterfalls for barriers that do not allow predators to reach sites upstream of these natural barriers. However, there is very little information on the temporal dynamics of the Northern range system (Magurran, 2005).

Species presence/absence is also potentially insufficiently informative for exploring predation pressure. The presence of a single predator can influence prey to a lesser degree than a large number of predators, and predator size affects which prey can be consumed. Individual species population sizes may also vary substantially without modifying a presence/absence list. Including estimates of predator abundance alongside presence/absence lists can consequently provide an additional level of detail for assessing risk to guppies, thus allowing for more nuanced assessments of potential dichotomies and temporal dynamics in predation levels. As with assemblage size, ensemble size can be quantified in terms of numerical abundance and biomass. Fish body size varies considerably between species and through ontogeny (Mittelbach *et al*., 1988), so estimates of predator ensemble size may vary substantially between numerical abundance and biomass values. Because of the strong influence of predation pressure on guppies and Trinidadian freshwater fish assemblages in general, it is important to ask whether different currencies of ensemble size affect our perception of predator pressure. Because predator pressure is assumed to vary based on waterfalls forming barriers to larger predators, it is possible that predator population sizes may be similar in high and low predation sites, but that body size and therefore biomass will be much lower in low predation sites. If one currency suggests a dichotomy in predator ensemble size while another suggests a gradient, then the choice of currency has the potential to influence our perception of predator pressure and thus our understanding of a mechanism driving assemblage composition and structure.

An additional consideration when measuring guppy predator pressure is which fish species to include as "predators". Historically, the species that researchers paid the most attention to were the larger predator species: the wolf fish *Hoplias malabaricus* and the pike cichlid *Crenicichla frenata* (Farr, 1975). Which species should count as guppy predators, however, is not clear cut because some smaller fish species still consume small or juvenile guppies (Mattingly and Butler, 1994). Including these smaller fish species in predation estimates, though, may mask the effect of waterfalls because they do not form effective barriers for smaller fish. Including abundance estimates in estimating predation pressure using different lists of species has the potential to introduce more uncertainty into the dichotomy/gradient question. Broader definitions of predators include larger fish like the wolf fish (maximum size of 560 mm; Phillip *et al*., 2013) alongside much smaller fish like *Anablepsoides hartti* (maximum size 110 mm; Phillip *et al*., 2013). Narrower definitions, including only the largest and most voracious predators, will have narrower body size distributions with higher average values. It is

therefore necessary to test results for a range of predation definitions to gain a more complete understanding of how the inclusion of numerical abundance and biomass values effects estimations of predation pressure.

3.2.1 Questions

In this chapter I ask two sets of related questions about how numerical abundance and biomass change. My first question uses a meta-analysis across assemblages, and aims to assess how change in assemblage size measured as numerical abundance and assemblage size measured in biomass relate. By assessing the relationship between numerical abundance and biomass change, I test for signals of decreasing body size which is a potential mechanism for change in assemblage size.

I expect to find no evidence of a decrease in numerical abundance across assemblages, in line with a previous meta-analysis by Dornelas *et al*., (2014). I expect biomass, on the other hand, to be generally decreasing, because smaller individuals will be increasingly replacing large individuals (**Figure 17A**). This hypothesis is based on the assumption that species with smaller body sizes tend to reproduce quicker (Cardillo, 2003) and have generally more r-selected life strategies (Pianka, 1970), which allows them to more easily thrive under increasing disturbance than their larger counterparts. This situation is plausible given the general increase in many disturbance types across assemblages that assemblages are undergoing as a consequence of anthropogenic activities, because fast reproduction will allow smaller species to recover more quickly from perturbations. This shift in life history strategies towards species that reproduce more quickly and so recover more rapidly from disturbances will be reflected in a decrease in biomass as average body sizes decline.

How assemblage size is changing in terms of both numerical abundance and biomass may vary across assemblages. For example, marine fish assemblages may be experiencing a greater decline is assemblage size in terms of biomass but not assemblage size as a consequence of overharvesting large individuals (Duplisea and Castonguay, 2006) and responses to climate change (Daufresne *et al*., 2009). Amphibian assemblages may be undergoing particularly severe decreases in assemblage size in terms of numerical abundance, as amphibian species population trends are declining more rapidly than either mammal or bird species (Stuart *et al*., 2004). Information on whether different realms of taxa are undergoing particular trends in assemblage size would help elucidate different threats

and reactions in different assemblages, and assist with choosing appropriate measures of assessing biodiversity change for different systems.

I therefore ask the questions:

1. Is biomass generally decreasing, and numerical abundance remaining consistent across assemblages?
2. Are there different trends in assemble size across different realms or taxa?

For the second part of my analysis, I focus on a case study of how numerical abundance and biomass relate when measuring a mechanism influencing assemblage structure. In this analysis, I explore different currencies of measuring the size of the guppy predator ensemble in Trinidadian rivers. Generally, I ask how the choice of currency (numerical abundance/biomass) affects perception of predation risk to guppies. Numerical abundance and biomass could provide quite different estimates of predation pressure across sites. This is because the mechanisms that mainly influences predation pressure is believed to be waterfalls that stop larger predatory fish from accessing areas upstream of these structures (Haski*ns et al*., 1961). Lower predation sites upstream should consequently consistently contain smaller predators than high predation sites. Smaller predators may, however, live at higher densities than larger predators, and all predator populations may fluctuate substantially due to population dynamics and predator-prey interactions. Therefore, I expect biomass to be lower for lower predation sites. Numerical abundance, however, will be more variable because population sizes will vary and be less affected by barriers to large predator migration. For example, a low predation site may have the same numerical abundance as a high predation site, but body sizes will still be lower so biomass will also be lower in low predation sites. Because body size varies substantially (orders of magnitude) between small and large predators, biomass should therefore still indicate a high or low predation site, even when population sizes vary.

Specifically, I ask two linked questions:

1. Is there more evidence for a dichotomy rather than a gradient of predation pressure in sites when predator ensemble size is measured in terms of biomass rather than numerical abundance?
2. Are site rankings more consistent over time when predator pressure is quantified in terms of biomass rather than numerical abundance?

3.3 Meta-analysis

3.3.1 Methods

For the meta-analysis of assemblage size across assemblages, I used the BioTIME database (Dornelas *et al*., 2018). When I undertook this analysis, this database contained 325 studies of assemblage size, measured in numerical abundance and/or biomass. The 6 545 000 individual records spans over 30 different ecoregions, and include assemblages from marine, freshwater and terrestrial biomes (**Figure 15**). The majority (263) studies quantify assemblage size in terms of numerical abundance only, whereas 20 studies contain only biomass data. The remaining 63 studies quantified assemblage size in terms of both abundance and biomass. The term biomass is an umbrella for various methods of quantifying size or weight. Within the BioTIME database, 10 different types of biomass are recorded, including cover estimates, wet and dry biomass and size proxies such as snout vent length (**Table 6**). The data for assemblage ID 45 were removed from analysis at this point, because biomass only was estimated from abundance (count estimated size) instead of being directly measured.

Table 6. The variety of quantification methods in the BioTIME database recording biomass of organisms.

Biomass measurement	**Assemblage count** **All assemblages**
Weight	35
Above ground biomass	19
Aggregated weight	5
Biovolume	3
Count estimated size	1
Snout vent length	1
Percent composition	1

To be included in the BioTIME database (Dornelas *et al*., 2018) a dataset must fit the following criteria: 1. The fundamental unit of observation must be a record of abundance of a species at a particular location and time; 2. All the records that belong to the same sampling event (location and time) are included in a sample; 3. Samples from the same location, but different

times, are considered from the same plot (not all studies resample at exactly the same location each time, so not all dataset contain plot level data); 4. Multiple plots and samples can be located at the same site; 5. The highest level of aggregation is the study. A study targets the same taxa in the assemblage, and has regular and consistent sampling methodologies.

The spatial scale of the assemblages varied over several orders of magnitude from 1mm^2 through to over 100, 000km^2. I decided to retain the integrity of the studied assemblages despite different spatial extents, however, because the original data collectors chose the spatial extent and grain based on expert knowledge of the taxon and system. The body size of the taxa surveyed also varies substantially (from plankton to whales), so there was not a single spatial scale that would appropriately capture the population and ecosystem dynamics of all the assemblages. In addition, by not splitting any datasets, I avoided spatial autocorrelation within studies.

I tested the trends in numerical abundance and biomass using the full datas*et* of assemblages that that had numerical abundance data (263 assemblages) for the numerical abundance analysis, and biomass data (83 assemblages) for the biomass analysis. To account for sampling differences between years, I used sample based rarefaction (**Figure 18**; Dornelas *et al*. 2014). Years with fewer than half the mean number of sampling occasions within that study were excluded from the analysis. Rarefied sample assemblage size was then summed per year for each sampled assemblage.

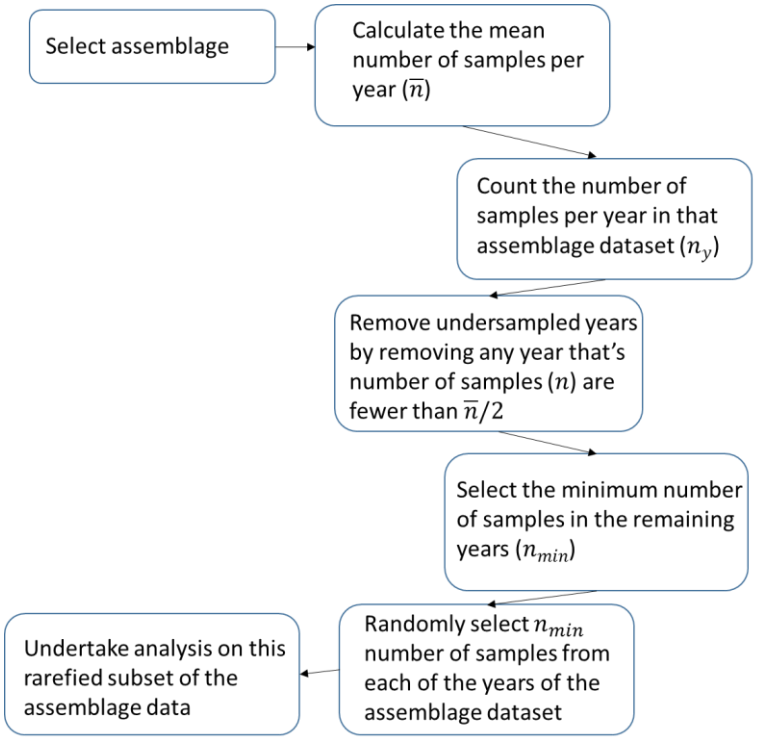


Figure 18. Workflow showing the process of rarefying a single assemblage in the BioTIME database.

I assessed general trends in assemblage size across assemblages using random mixed effects models. The random slopes of the best-fitting models were used to extract individual assemblage rates of change, and a single overall slope was calculated for the general trends. Numerical abundance was transformed before analysis using $\log_2$ transformations to allow for better comparison of studies with different size taxa. In the case of biomass, some values were less than 1, so $\log_2$ x+1 was used instead. The numerical abundance or biomass each year was regressed against mean-centred year, with Assemblage ID included as a random effect with varying slope and intercept (**Equation 1**). I tested for differences between realms and taxonomic groups by using AIC fitting on of a variety of different model constructions (**Equation 2**). The model with the lowest AIC value was selected. I considered two models with AIC values differentiated by at least 2 to be different. I did not test for the effect of measurement type on biomass results because there were too few data points in some of the categories (**Table 6**). In addition, I plotted the rate of change for each assemblage size trend against the length of the study to check for an influence of study length.

Equation 1. The linear mixed model used to calculate rates of change of assemblage size. Model fit plots for numerical abundance (a) are shown in **Appendix Figure 1** and biomass (b) in **Appendix Figure 2**.

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

η_i is the assemblage size for value i, quantified in terms of either (a) $\log_2$ numerical abundance or (b) $\log_2$ biomass

x_i is the mean centred year for value i from dataset n

α is the overall intercept

β is the overall slope for mean centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is the residual error

Equation 2. The linear mixed model used to calculate rates of change of assemblage size, with realm or taxonomic group included as a fixed effect. The effect of the type of biomass measurement used (**Table 8**) was also tested for the biomass data. The model was run with and without an interaction effect term. There were consequently 8 models constructed: a1) abundance with realm but no interaction, a2) abundance with realm interacting with mean-centred year, a3) abundance with taxonomic group but no interaction, a4) abundance with taxonomic group interacting with mean-centred year, b1) biomass with realm but no interaction, b2) biomass with realm interacting with mean-centred year, b3) biomass with taxonomic group but no interaction, b4) biomass with taxonomic group. The model fit for Equation a3) and b3) only are provided (**Appendix Figure 3** and **4**, respectively) because the other models were not used for further analysis.

$$\eta_i = \alpha + \beta x_i + m_r l_r + d(x_i + l_r) + b_j + S_j x_i + \epsilon_i$$

η_i is either the $\log_2$ numerical abundance or the $\log_2$ biomass for value i,

x_i is the mean-centred year for value i from dataset n

α is the overall intercept

β is the overall slope for mean-centred year x

l_r is the additional fixed effect (either realm or taxonomic group) type r for value i,

m_r is the overall slope for change in fixed effect (either realm or taxonomic group) type r

$d(x_i + l_r)$ is the interaction between mean-centred year and fixed effect r

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is the residual error

To evaluate whether the trend in assemblage size remained consistent across assemblage size currencies, I selected only the 63 assemblages that had data for both abundance and biomass. I analysed the correlation between the two currency trends by assessing Pearson's Coefficient and Spearman's Rank, calculated using the *cor.test* function in R.

3.3.1 Results (BioTIME data)

The best model for both the abundance data and the biomass data included a fixed effect of taxonomic group with no interaction effect (**Table 7**). The results of the abundance and biomass models are therefore calculated from these two models (**Equation 2a.3** and **Equation 2b.6**, respectively), and not from the simpler models presented in **Equation 1**.

Table 7. The AIC values of the different models of assemblage size regressed against mean-centred year, used between each AIC value and the lowest value to select the best fitting model for each assemblage size currency. Values are expressed as ΔAIC between the lowest AIC value and each other model AIC. Full details on model construction can be found in **Equation 1** and **Equation 2**.

Assemblage Size Currency	Additional Fixed Effect	Interaction Effect	Equation	ΔAIC
Numerical Abundance	None	No	2a	37
	Realm	No	3a.1	19
	Realm	Yes	3a.2	4
	Taxa	No	3a.3	0
	Taxa	Yes	3a.4	49
Biomass	None	No	2b	23
	Realm	No	3b.1	21
	Realm	Yes	3b.2	32
	Taxon	No	3b.3	0
	Taxon	Yes	3b.4	33

I detected no significant change in the trend for either abundance (slope: 0.0051, SE: 0.0054, **Figure 19A**) or biomass (slope: -0.01, SE: 0.020, **Figure 19B**). The trends for both currencies were not different across realms (**Figure 20**), nor strongly affected by the length of study (**Figure 21**). Although including taxonomic group in the both the abundance and biomass data model improved model fit significantly (**Table 7**), neither of these models included an

interaction effect with mean-centred year. There were therefore no significant differences in trend across different taxonomic groups for either abundance or biomass (**Figure 22**).

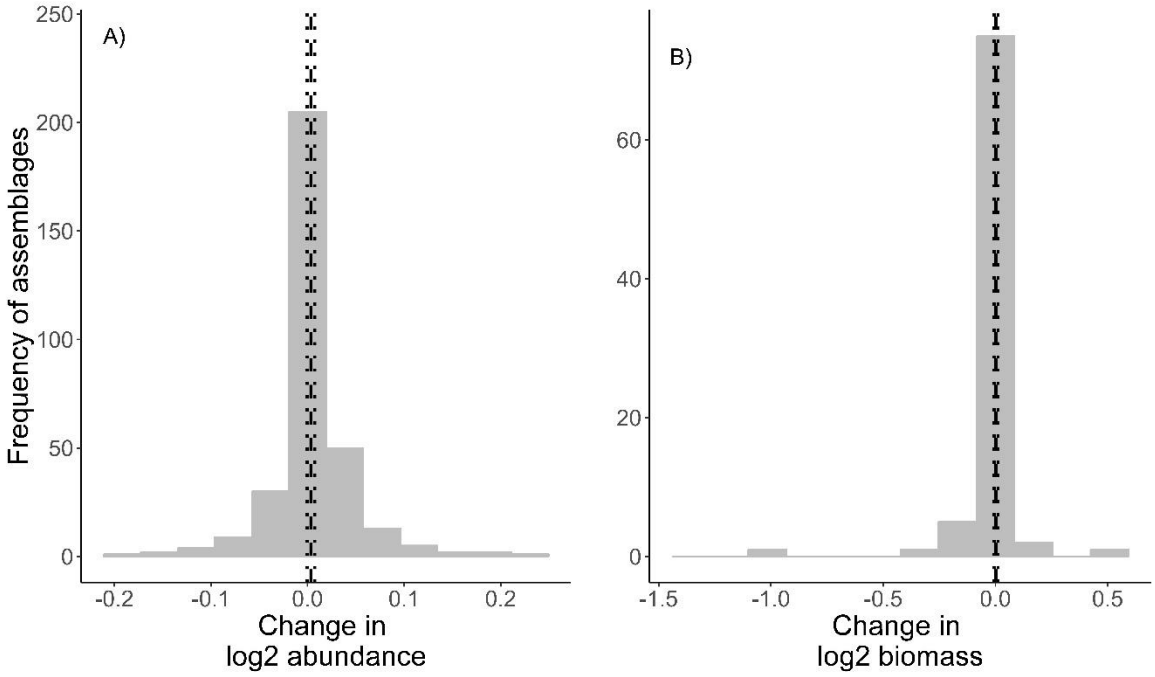


Figure 19. Histograms of rates of change of (A) l log_2 numerical abundance and (B) log_2 biomass. The dashed lines represent the overall trend of the models, and the dotted lines represent the standard error around these estimates.

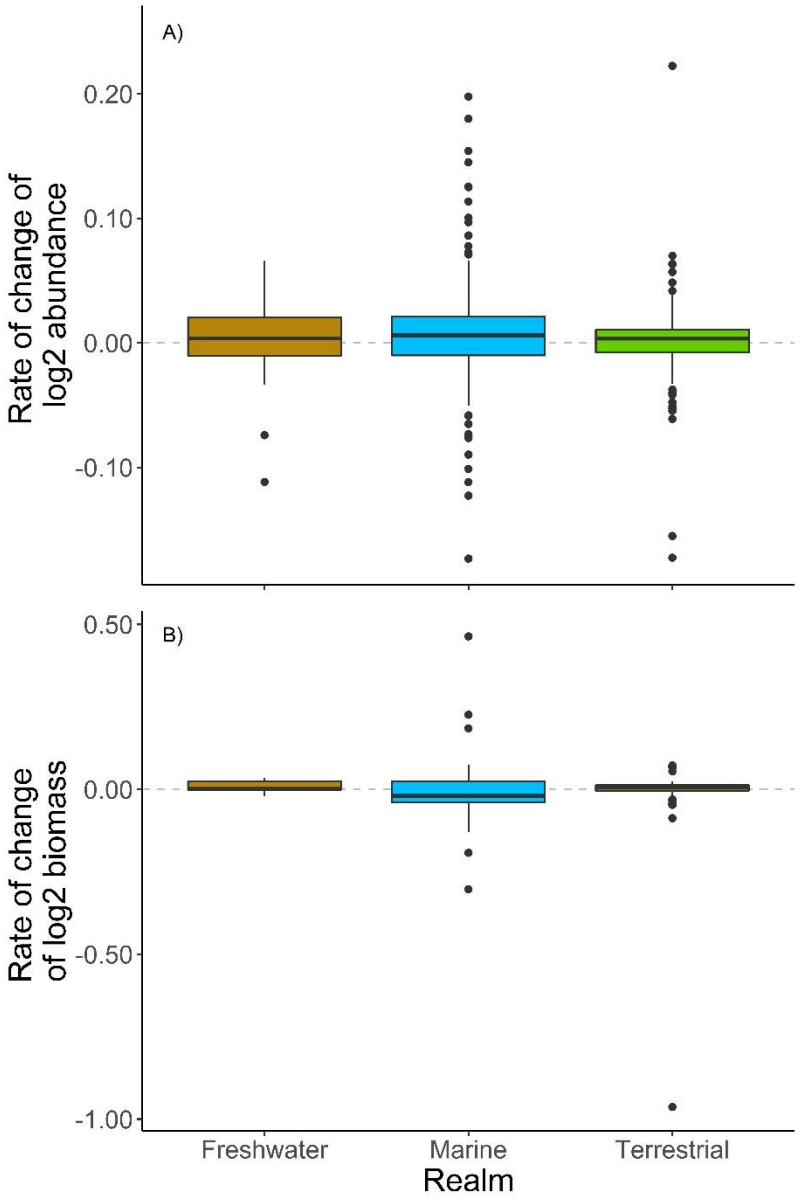


Figure 20. A box plot showing the first and third quartiles (boxes), and ranges (whiskers), and median (horizontal line) of the trends in (A) numerical abundance and (B) biomass, split by realm.

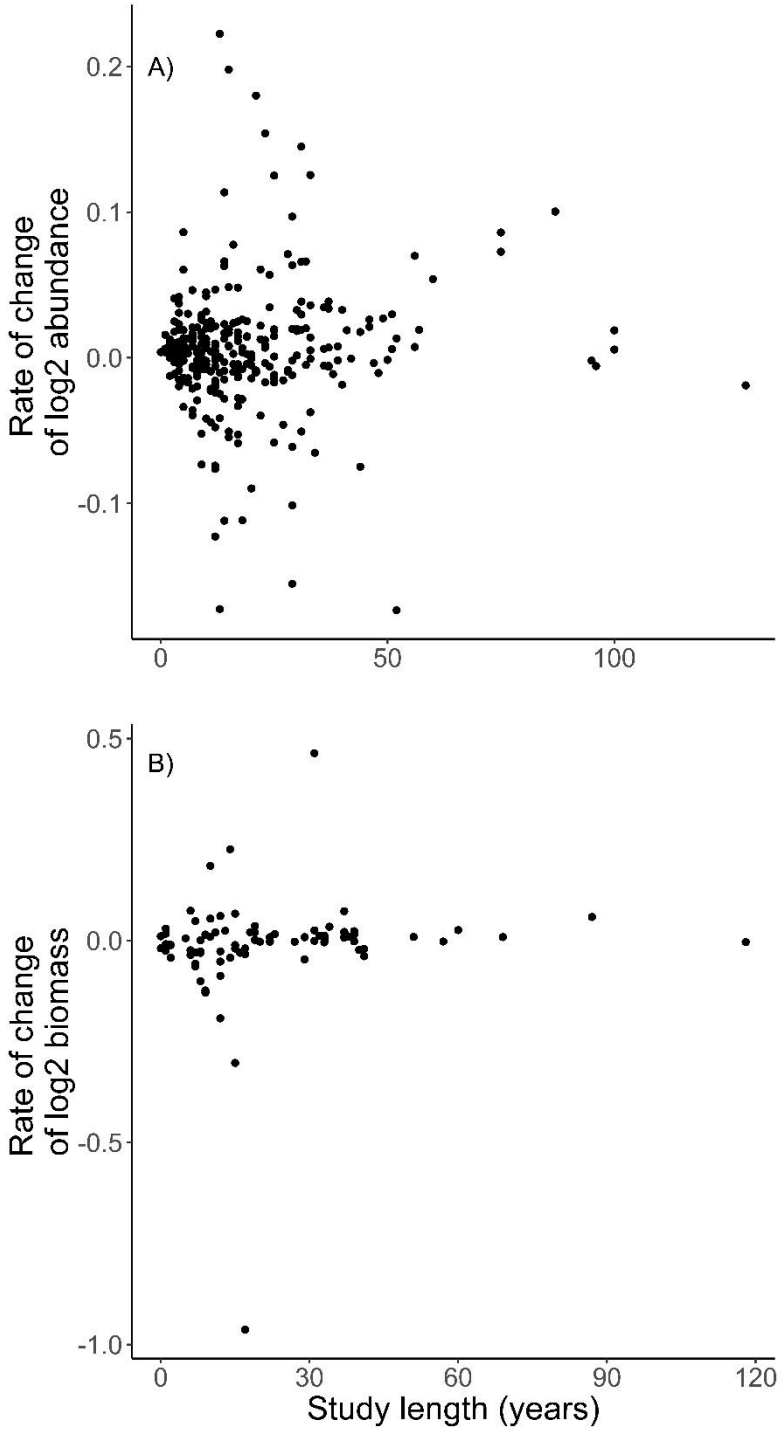


Figure 21. Scatter plots of the trends in (A) $\log_2$ numerical abundance and (B) $\log_2$ biomass change against assemblage timeseries length

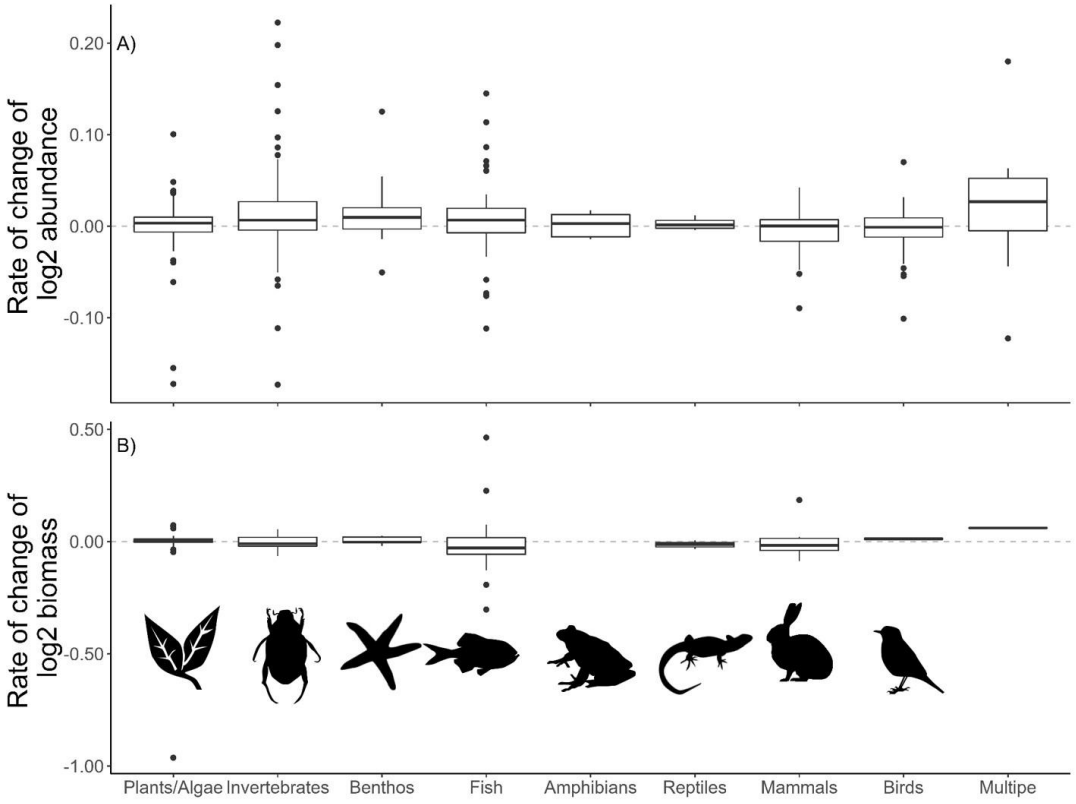


Figure 22. A box plot showing the first and third quartiles (boxes), and ranges (whiskers), and median (horizontal line) of the trends in (A) $\log_2$ numerical abundance and (B) $\log_2$ biomass, split by taxonomic group. There are no data for trends in amphibian biomass.

The trends in numerical abundance and biomass change within each assemblage were positively correlated (Pearson's correlation 0.43, p: <0.001, Spearman's Rank 0.53 p: <0.001, **Figure 23**). The trend is linear, with the exception of assemblage 235, which is a terrestrial plant assemblage that shows a much greater decrease in biomass than numerical abundance.

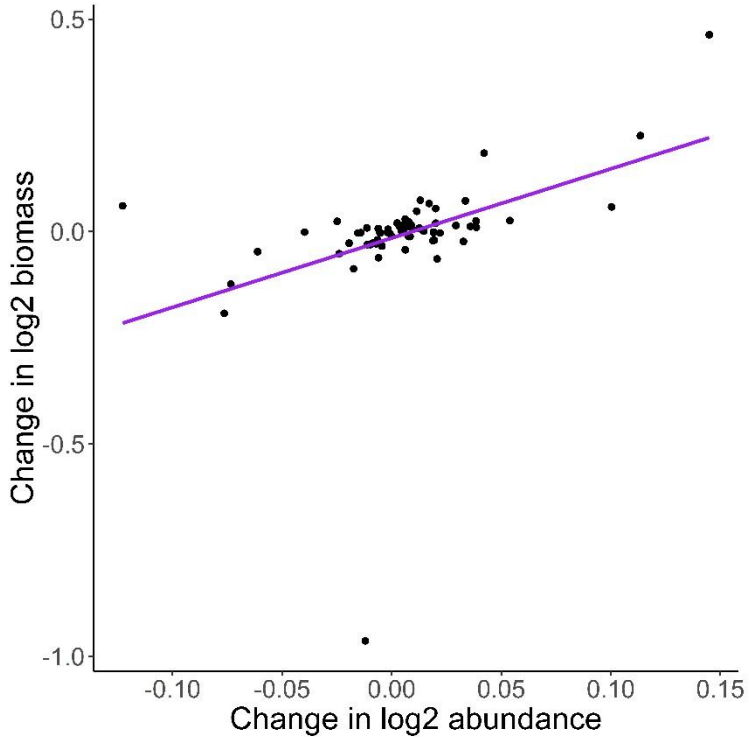


Figure 23. The relationship between slope of change in log_2 numerical abundance and slope of change in log_2 biomass, for the 63 assemblages where assemblage size is recorded in both currencies.

3.4 Case Study

3.4.1 Methods

A total of 16 sites spread between 8 different rivers along the southern slopes of Trinidad's Northern Range were sampled once a year (July/August) for 6 years between 2011 and 2016 (**Figure 16**). To minimise the effects of diurnal variation, surveys always took place between 8.00am and 11.00am. This sampling was undertaken by Dr Deacon and her team of field assistants. Data were collected for the BioTIME project to assess assemblage change over time. For full methodological information see Deacon *et al*., (2018) and Magurran *et al*., (2018). I assisted with data collection for the 2015 season.

Each site was a 50m stretch of stream that was blocked at both ends by seine nets. To gain as complete as possible sample of the fish assemblage in each site, each stretch was systematically fished from one end to the other using first a two-handed seine (64 mm mesh) and then again with electrofishing equipment. Once caught, fish were stored in shaded buckets, with predators and prey separated wherever possible. Each fish (except for guppies)

was then identified and weighed, before being returned to the stretch of stream. Because guppies were so numerous and small, they were categorised as mature female, mature male, or juvenile, and typical weights were then used to estimate biomass.

To assess how sensitive my results are to the definition of predation, I used three alternative categories of predation based on trophic classifications using available information on diet (Kenny, 1995; Phillip *et al*., 2013). The first category takes a "narrow" view of what a guppy predator is, including only 2 "strong piscivorous" species widely acknowledged to be the main predators of guppies: *Hoplias malabaricus* and *Crenicichla frenata*. The second "intermediate" view includes an additional 2 species that are considered "moderately piscivorous." Finally, the "broad" view encompasses even those fish classified as "weakly piscivorous" (**Table 8**).

Table 8. The species of fish used to define each level of guppy predation. "Narrow" includes only the 2 most strongly piscivorous species, "intermediate" includes an additional 2 moderately piscivorous species, and the broad category includes all piscivorous fish in the system

Scientific name (and authority)	Common name	Narrow	Intermediate	Broad
***Crenicichla frenata* (Gill 1858)**	Pike cichlid	X	X	X
***Hoplias malabaricus* (Bloch 1794)**	Wolf fish/Guabine	X	X	X
***Anablepsoides hartii* (Boulenger 1890)**	Hart's killifish		X	X
***Gymnotus carapo* (Linneaus 1758)**	Cutlass fish/Knifefish		X	X
***Agonostomus monticola* (Bancroft 1834)**	Mountain mullet			X
***Andinoacara pulcher* (Gill 1858)**	Blue acara/Blue coscorob			X
***Cichlasoma taenia* (Bennett, 1831)**	Brown acara/Brown coscorob			X
***Corynopoma riisei* (Gill 1858)**	Swordtail sardine			X
***Hemigrammus unilineatus* (Gill 1858)**	Featherfin tetra			X
***Rhamdia quelen* (Quoy and Gaimard 1824)**	River catfish/Silver catfish			X

In this analysis, I assume that predation risk is directly correlated with the presence and abundance of predators (Reznick and Endler, 1982). To assess predation risk at each site, I therefore calculated predation pressure (measured in numerical abundance and biomass) for each site and each definition of predation. Numerical abundance was defined as the total

number of individuals, and biomass was the total wet weight (g) of all individuals of the species in a category. Numerical abundance was $\log_2$ transformed, and biomass was $\log_2 + 1$ transformed before analysis. The exception to this was the Kendall concordance test, where untransformed values were used. All analysis took place in R (R Core Team, 2018).

To answer the question of whether sites are ranked consistently between currencies in terms of predation pressure, I first constructed box plots for each of the scenarios and currencies based on mean annual predation values for each site. Sites were placed along the x-axis in order of predator abundance or biomass, so I could assess whether the sites lie along a gradient of predation pressure or represent a dichotomy. A gradient would be represented by a continuum of sites, ranging from high to low, whereas a dichotomy would be represented by distinct groupings of sites. For the second part of this analysis, I assessed the consistency in site ranking using a Spearman's Rank correlation and by constructing tanglegrams using the *plot* function in R. Sites were ordered in terms of decreasing mean predator abundance over the entire 6-year sampling period, with the sites with the highest values at the top of the tanglegram. The relationship between currencies was assessed for each predation category.

I assessed whether rankings in predation pressure using both currencies persisted over time by using a Kendall concordance test using the *kendall.global* function in the *vegan* R package (Oksanen *et al*., 2017). The untransformed abundance and biomass data were used for the Kendall concordance test because the ranking of site predator pressure does not rely on relative differences between sites. I also modelled trends over time using linear mixed effect models with the *lme4* R package (Bates *et al*., 2015). I constructed a linear mixed effect model for each predation level and both numerical abundance and biomass. In each of these 6 models, the size of the predation pressure was regressed against mean-centred year, with site included as a random effect (**Equation 3**). Individual trends for each study were then extracted for visual analysis using line plots.

Equation 3. The linear mixed model used to calculate rates of change of predation pressure. Model fit plots in (a) **Appendix Figure 5**, (b) **Appendix Figure 6**, (c) **Appendix Figure 7**, (d) **Appendix Figure 8**, (e) **Appendix Figure 9**, (f) **Appendix Figure 10.**

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

η_i is the size of the predation pressure that year for a) numerical abundance with narrowly defined predation, b) numerical abundance with intermediately defined predation, c) numerical abundance with broadly defined predation, d) biomass with narrowly defined predation, e) biomass with intermediately defined predation, and f) biomass with broadly defined predation

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect of site j

S_j is the change in slope for values with the random effect j

ϵ_i is residual error

3.4.2 Results (Trinidadian fish data)

Contrary to my expectation, plots of $\log_2$ numerical abundance and biomass illustrate that predation level is a gradient rather than a dichotomy along the 16 sites for both currencies of predator ensemble size (**Figure 24**). Where there was some evidence of separation of sites (e.g. the two lowest predation sites UA1 and UA2 for the narrow category of predation) the site placement was consistent between numerical abundance and biomass measurements.

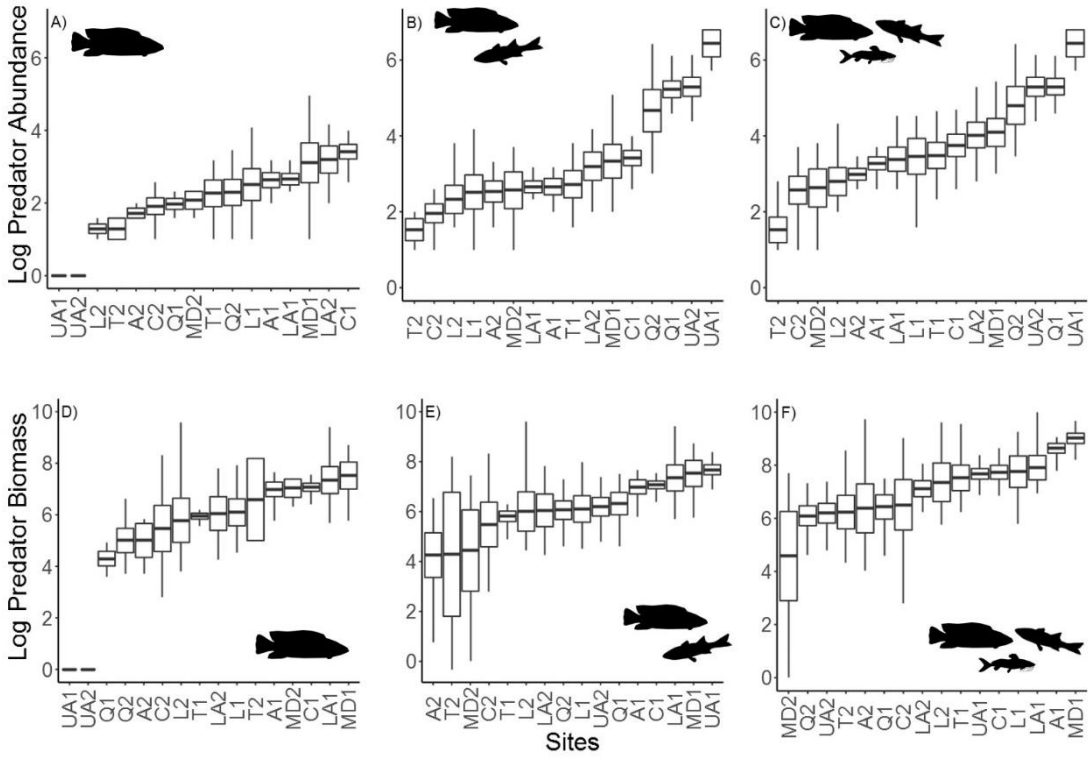


Figure 24. The mean values, standard errors (boxes), and ranges (whiskers) for 6 time points for each site, for $\log_2$ predator numerical abundance (upper row) and $\log_2$ predator biomass (lower row) for the 3 categories of predators: A) abundance narrow, B) abundance intermediate, C) abundance broad, D) biomass narrow, E) biomass intermediate and c) biomass broad. Sites are plotted in rank order along the X-axis. See **Figure 16** for key to the site codes.

For narrow estimates of predation pressure, sites were ranked consistently along the gradient for numerical abundance and biomass measurements (r_s: 0.65; *P:* 0.007; **Figure 25A**). In contrast, there was no significant consistency in site ranking between numerical abundance and biomass measurements for intermediately and broadly defined predator ensembles (Intermediate: r_s: 0.21; *P:* 0.443; Broad: r_s: −0.11; *P:* 0.680; **Figure 25B** & **Figure 25C**).

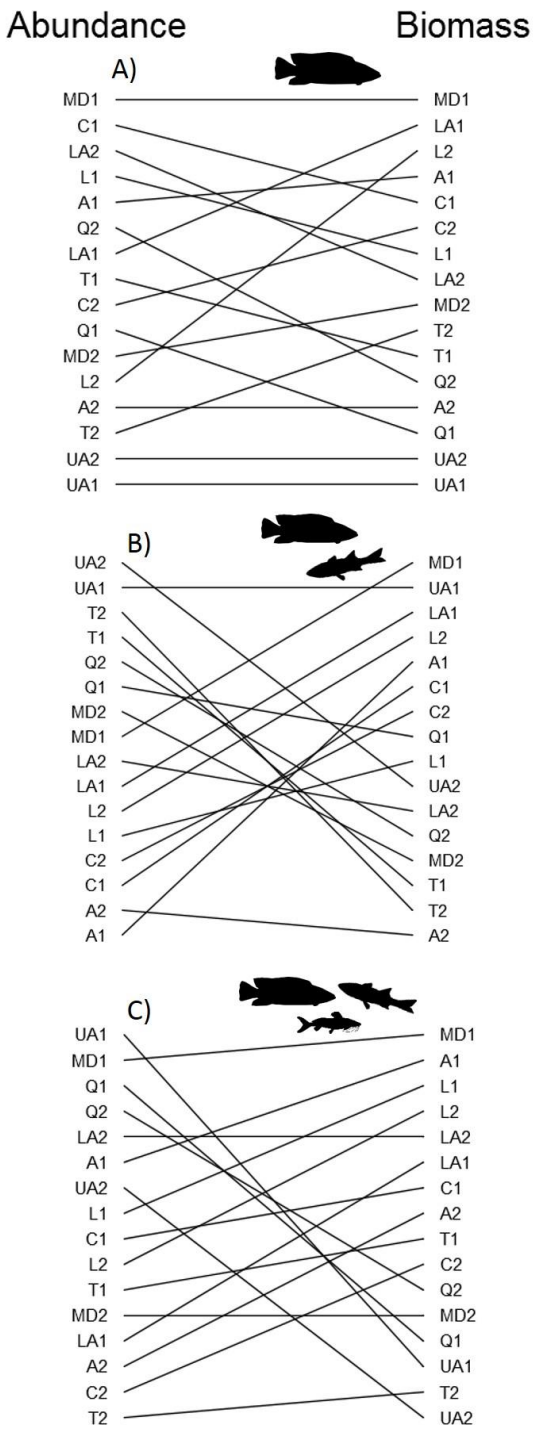


Figure 25. Tanglegrams depicting the consistency of predation pressure ranking between numerical abundance and biomass estimates for the A) narrow, B) intermediate, and C) wide definition of predation. Sites are ordered in descending predation pressure. Sites rankings are significantly correlated only for the intermediate (A) definition of predation.

There were no strong trends in predator pressure over time for either numerical abundance or biomass, although there is a suggestion of an increase in predator numerical abundance for intermediately and broadly defined predation levels (**Table 9**). There was considerable variation in the level of predation pressure over time within sites for all categories and currencies of predation. Different sites show different trends, but in general the site rankings remained consistent over time regardless of the approach to quantifying predation pressure (**Figure 26**). This result is reflected in significant Kendall concordance scores for rankings over time for almost all approaches (**Table 9**). Intermediately defined predation using biomass was the exception to this temporal consistency.

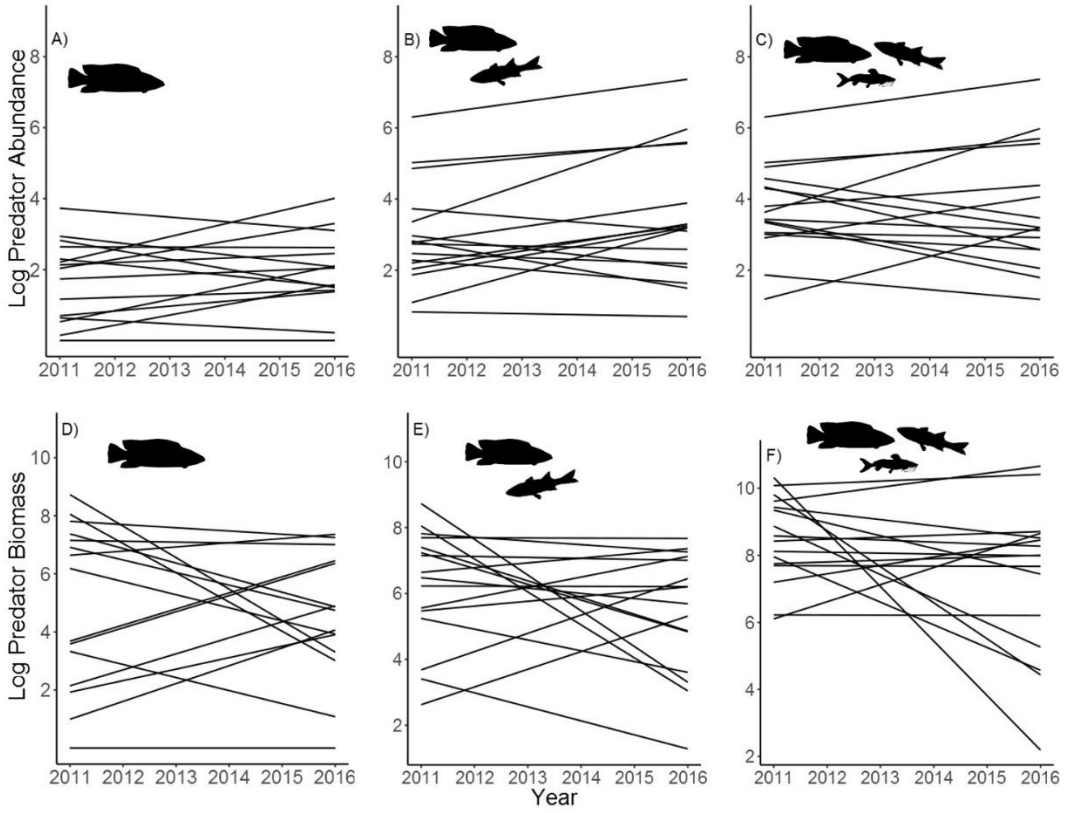


Figure 26. The trends over time in log_2numerical abundance or log_2 biomass for sites, as calculated from individual mixed effect models for each panel. Each line represents the rate of change for a single site using that currency and definition of predation. Results are shown for the 3 categories of predators: A) numerical abundance narrow, B) numerical abundance intermediate, C) numerical abundance broad, D) biomass narrow, E) biomass intermediate and c) biomass broad.

Table 9. Kendall Concordance values, and the overall mixed model trend and standard error, for each predation level and currency.

	Kendall Concordance (W)		**Mixed model Linear trend**	
	Abundance	**Biomass**	**Abundance**	**Biomass**
Narrow	0.35 (p < 0.001)	0.30 (p 0.006)	0.04 (T 0.80)	-0.08 (T -0.58)
Intermediate	0.62 (p <0.001)	0.22 (p 0.052)	0.10(T 1.66)	-0.15 (T -0.29)
Broad	0.62(p < 0.001)	0.31 (p < 0.001)	0.01 (T 0.14)	-0.23 (T -0.16)

3.4. Discussion

3.4.1 Meta-analysis

In non-transitional habitats, assemblage size has been theoretically predicted and empirically observed to be far more stable than species composition or population abundances (i.e. Ernest and Brown, 2001; Gotelli *et al*., 2017; Lehman and Tilman, 2000; Supp *et al*., 2012). In line with this assumption, my results show that irrespective of currency, there is no evidence of a general decline in assemblage size globally. When there is a change in assemblage size abundance, numerical abundance and biomass both change in the same direction (**Figure 21**). In this section of the discussion, I will consider some of the potential explanations for the generally un-trending numerical abundance and biomass measurements of assemblage size, and reflect on the implications for the relationship between these two currencies of abundance.

One possible explanation for the lack of trend on average of assemblage size detected in my study is that the assemblages included in the BioTIME dataset are not located in transitional habitats (Dornelas *et al*., 2018). Cases where extreme disturbances take place, for example clear-felling for agriculture, are consequently not included in my analysis. Assemblage size under such drastically changing conditions is likely to be decreasing as conditions change too quickly for adaptation to take place. However, the effects of anthropogenic activities are so pervasive that it is highly unlikely that any assemblages are unaffected. For example, to some extent climate change affects all ecosystems, and ocean acidification affects all marine systems. My results are therefore unlikely to be caused by selecting assemblages in locations that are not transitional habitats, because even the relatively unmodified assemblages in the BioTIME database are will all be influenced to some extent by anthropogenic pressures.

There is little consensus on the exact mechanisms underpinning stability within assemblages. One possible mechanism is if the loss of species unsuited to new conditions are compensated by increases in other species more well suited to the new conditions (Gonzalez and Loreau, 2009; Supp and Ernest, 2014). Such compensatory dynamics select for more stress-tolerant species, because stress-tolerant species are more likely to adapt to new conditions or disturbances (Ives and Cardinale, 2004). Compensatory dynamics are predicted to have a strong stabilising effect on assemblage level properties (Gonzalez and Loreau, 2009) and have been detected in natural systems (Vasseur and Gaedke, 2007). However, general empirical evidence of such regulation is rare (Houlahan *et al*., 2007).

An alternative explanation for assemblage size stability, even under changing conditions, is the portfolio effect (Doak *et al*., 1998; Lhomme and Winkel, 2002). This mechanism predicts that species rich assemblages will experience stable assemblage size because the different population trends of different species will average out to no directional trend. This statistical averaging is in part a consequence of the diversity of features amongst species in species-rich assemblages (Schindler *et al*., 2015), but it does not rely on species directly compensating for each other. For example, assemblage regulation can be partly underpinned by the varying dynamics between guilds (Magurran and Henderson, 2018). Although different guilds may exhibit substantial variation in numerical abundance and biomass, as demonstrated by my case study of predatory fish in Trinidadian rivers, the combination of different guilds' fluctuations and resource competition may cause independent fluctuations that average out to un-trending assemblage level properties. As with the compensatory dynamics, however, evidence for the portfolio effect is mixed (Houlahan *et al*., 2018).

The un-trending nature of assemblage size generally detected by my analysis is unlikely to be a consequence of a single mechanism. The importance of different mechanisms can vary across environmental gradients (Hallett *et al*., 2014). Disentangling the relative contributions of different stability mechanisms across varied assemblages would help clarify how assemblages react to change, but is beyond the scope of this analysis. Irrespective of which mechanism underpins assemblage size stability, there is great potential for shifts in species identities and consequently ecosystem functioning. How well a species can adapt to new environments and increasing disturbance levels is an important characteristic in determining how well species will fare under habitat change. Generalist species can, by their very definition, utilise a broader range of resources and so are more likely to adapt. For example,

the abundance of generalist reef fish did not decline in a study of coral reef degradation whereas specialist species underwent decreases in numerical abundance (Alvarez-Filip *et al*., 2015). Generalist species immigrating into new assemblages can also outcompete resident species, and so drive biotic homogenisation (Olden *et al*., 2004). I found that that biomass is not generally decreasing, which suggests that smaller individuals are not generally replacing larger individuals across assembles. I explore the question of shifting body size further in *Chapter 4*. However, the increasing turnover within assemblages detected by (Dornelas *et al*., 2014) suggests that even though I find little evidence of assemblage size change, there may still be substantial shifts in species composition and functioning.

Although there is no general trend in assemblage size, there is substantial variation in the trend of assemblage size change between individual assemblages. In many cases, assemblage size (in terms of both numerical abundance and biomass) increased or decreased. Assemblage size is a product of the energy available in an area, combined with the ability of species within the assemblage to use resources under the environmental conditions of the ecosystem (Brown *et al*. 2001). For there to be a change in this assemblage property, there must therefore be either a change in energy availability or assemblage energy efficiency. That there are shifts in assemblage size in many cases is concerning, because it suggests substantial shifts in ecosystem functioning. Understanding how change in the two different currencies relate in these cases could provide further information on the changes taking place, and how they may affect ecosystem functioning.

A theory indicating the close relationship between numerical abundance and biomass is the energetic equivalence rule, otherwise known as Damuth's Rule (Damuth, 1981). This rule suggests that small species will live at higher densities than large species, and therefore be prevalent in higher abundances. However, at a local scale there is little evidence for a clear relationship between biomass and abundance (Blackburn and Gaston, 1997; White *et al*., 2007). This lack of relationship may be because Damuth's rule generally applies to taxa across many orders of magnitude, and such variety in body size may be lacking in local assemblages. In addition, species tend to be spatially aggregated (Taylor, 1961). If a species is on the edge of its range, or the sampling takes place away from aggregations of that species, then population density is likely to be lower than expected based on body size. My results support a lack of evidence for the energetic equivalence rule at a local scale because numerical abundance and biomass change in the same direction. When there are increases in

individuals, there are generally corresponding increases in biomass, and when there are decreases in numerical abundance there are also decreases in biomass. If Damuth's rule held true, no change in biomass would be expected with changes in numerical abundance, because individuals would be relatively smaller or larger based on changes in population density. That biomass changes directionally with numerical abundance suggests that changes in numbers of individuals are closely linked to changes in the overall resources available or used by assemblages, as opposed to representing reallocations of the same amount of resources. This result has implications for niche partitioning (Tilman *et al*., 2014), because it suggests that niche space (i.e. resource availability) is variable based on which species are present in an assemblage.

My results suggest that increasing numerical abundance of small individuals is not compensating for losses in large individuals. But this result is not evidence that there are no shifts in body size distributions across assemblages, particularly when some assemblages do show evidence of shifts in assemblage size. If declines in assemblage size are a consequence of losses of large individuals without increases in numerical abundance of smaller species, then numerical abundance and biomass should still positively co-vary despite a decrease in overall body size. Following the same reasoning, if increases in numerical abundance are driven by sufficient increases in the number of small individuals, then numerical abundance and biomass would both increase despite a decrease in overall body size. It is difficult to disentangle changes in numerical abundance and body size further while focusing on assemblage level properties. To gain further understanding of potential decreases in body size among assemblages, analysis of individual and species body size distributions are needed.

3.4.2 Case study

I found that trends in numerical abundance and biomass co-vary positively, which suggest that either currency can be used effectively to monitor changes at the assemblage level, but this result does not necessarily hold true for other aspects of assemblages. The results from my case study of guppy predators in Trinidadian rivers demonstrate how estimations of important mechanisms affecting assemblage structure, such as predation pressure, can vary according to the currency used. For intermediately and broadly defined predator ensembles, there was little correlation between site rankings using numerical abundance and biomass (**Figure 25A** & **C**). There was, however, some consistency between currencies for narrowly defined predator ensembles containing only the two largest predators (**Figure 25**). This

increase in consistency between currency site rankings may have been driven by the two lowest predation sites containing no large predators, and ranking lowest for both numerical abundance and biomass. Once more species were included in the definition of predator, there was opportunity for populations of smaller predators to compensate in terms of either numerical abundance or biomass for smaller or missing populations of large predators.

Irrespective of the breadth of the definition of predation, I found great variation in the gradient of predation risk across sites (**Figure 24**). Numerical abundance was also more consistent than biomass (**Figure 26**; **Table 9**), meaning the choice of abundance currency affected the temporal consistency of site rankings over time regardless of the category of predation used. One potential reason for this is that biomass is sensitive to the differences in body size between individuals. The movements of just a few large individuals in or out of a site will therefore have a considerable impact on the total biomass, but only a minor effect on the numerical abundance (Knouft, 2002). While large schools of small fish moving in and out of samples can strongly affect numerical abundance but not biomass, my results thus suggest that numerical abundance may be a more reliable estimate of where a site sits on the predation pressure gradient if a study will only estimate predation pressure on a single occasion. If schooling behaviour is common and influential, however, then this result may not be the case.

Studies at a local scales have found little evidence of a consistent relationship between numerical abundance and biomass (Ehnes *et al*., 2014; Saint-Germain *et al*., 2007; Stead *et al*., 2005; White *et al*., 2007). My results relating to guppy predators support these findings, because site rankings, in terms of predation risk, are not conserved across currencies for intermediate or broadly defined predation pressure. As such, this study adds more weight to the conclusion that numerical abundance and biomass cannot be assumed to be surrogates for one another in all ecological studies. When assessing mechanisms for assemblage structure, investigators thus need to make informed decisions regarding appropriate abundance currencies in the context of local knowledge and ecological processes. When estimating predation pressure, for example, consideration is needed as to whether it is the number of predators or the size of the predators that is the driving force behind the effects of predators on guppy populations.

3.4.3 Conclusion

In this chapter, I found evidence that in general assemblage size is remaining stable across different habitats, and that when assemblage size did change then trends in numerical abundance and biomass closely and positively correlated. Smaller individuals are therefore not generally replacing larger individuals. Although there was no directional change in assemblage size, there was substantial variation between assemblages; many of the assemblages analysed did increase or decrease in size. In addition, substantial changes in species identity could take place while assemblage size remains stable (Magurran and Henderson, 2010). For example, in fragmented rainforest patches, amphibian and reptile assemblages displayed changes in species identities and relative abundances without changing assemblage size (Russildi *et al*., 2016). My results therefore do not mean that assemblages are not changing as a response to increased anthropogenic pressures.

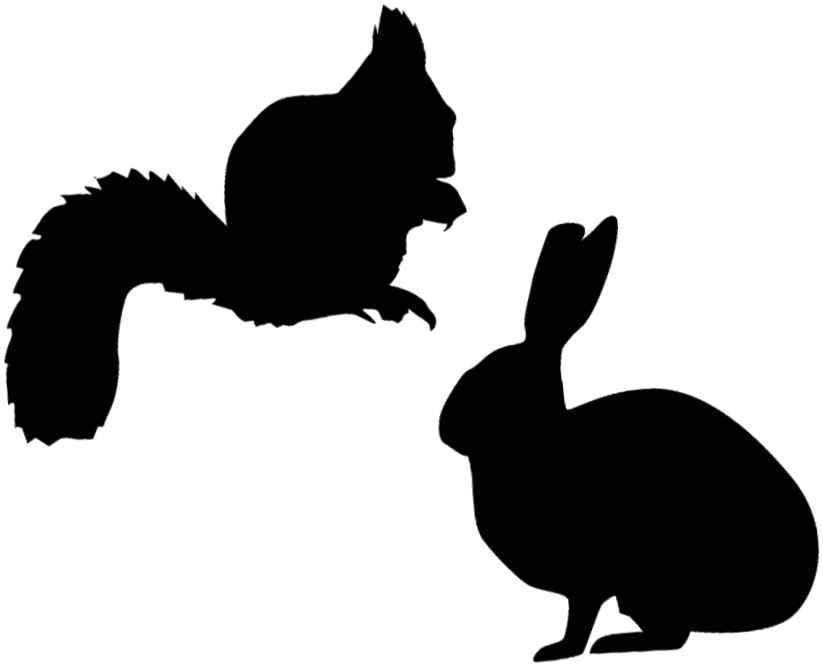
My results also highlight the fact that while at the assemblage size level, numerical abundance and biomass may be closely aligned, this relationship does not necessarily hold true for other aspects of assemblages. Estimations of the size of the predator ensemble amongst fish in Trinidadian rivers varied based on whether numerical abundance or biomass were used, and biomass estimates were more variable over time. Care therefore needs to be taken when measuring aspects of assemblages using either numerical abundance or biomass, despite my finding a close relationship between change in numerical abundance and change in biomass for measuring assemblage size. When seeking to understand the mechanisms that affect assemblage structure, numerical abundance and biomass can provide relatively different answers.

Although assemblage size is a fundamental property of an assemblage that is closely linked to aspects of ecosystem functioning, it is not the only influential aspect of an assemblage in relation to ecosystem functioning. My analysis thus far has ignored species identities and relative abundances, but not all species contribute equally to ecosystem functioning. For example, numerically dominant species often contribute substantially to ecosystem functioning (Gaston and Fuller, 2008; Lohbeck *et al*., 2016; Winfree *et al*., 2015), so changes in their numerical abundance or body size could strongly influence functioning irrespective of changes in assemblage size. Also, not all species are equally vulnerable within assemblages. Locally rare species, due to their small population sizes, are more vulnerable to disturbances than abundant species (Pimm *et al*., 1988). Although these species may only account for a

small proportion of the numerical abundance of an assemblage, substantial declines amongst them may decrease species richness and consequently functional richness. I will therefore assess changes in dominance structure and body size in *Chapter 4*, and changes in rare species in *Chapter 5*.

Chapter 4

Changes in the abundance, identity and size of dominant species



Parts of this study were published in the journal article:

Jones FAM, & Magurran AE (2018). Dominance structure of assemblages is regulated over a period of rapid environmental change. Biology letters. 14(6), 20180187. http://dx.doi.org/10.1098/rsbl.2018.018

4.1 Abstract

One of the few universal patterns in ecology is that one or a few very common species dominate assemblages. These numerically dominant species can contribute disproportionately to ecosystem services, so even a small change in their abundance or identity could have large consequences for ecosystem functioning and sustainability. In this chapter I aim to analyse systematic trends in the abundance and identity of dominant species across taxa and realms, to assess how this important aspect of assemblages is changing as a response to increasing anthropogenic pressures on the environment.

Contrary to my prediction of increasing dominance across assemblages, I found no evidence of any systematic trend in dominance. This lack of trend held true for all realms and taxonomic groups. In cases where the abundance of the dominant species did change, it generally tracked changes in assemblage size, thereby maintaining the dominance structure. That the relative abundance of the dominant species remained constant even when the assemblage size changed means the dominance structure was regulated (i.e. does not change directionally). In line with my prediction, however, I found evidence of change in terms of the identities of the dominant species; there was a trend in increasing turnover of dominant species identities. This increase in turnover did not translate into the expected corresponding shift in dominant species body size though; I found no evidence that small dominant species were replacing larger dominant species across mammal, amphibian, bird and fish assemblages. I did, however, find evidence of within-species body size declines amongst the dominant species of a subset of fish assemblages that contained individual body size. My results suggest that body size shifts are taking place within species populations.

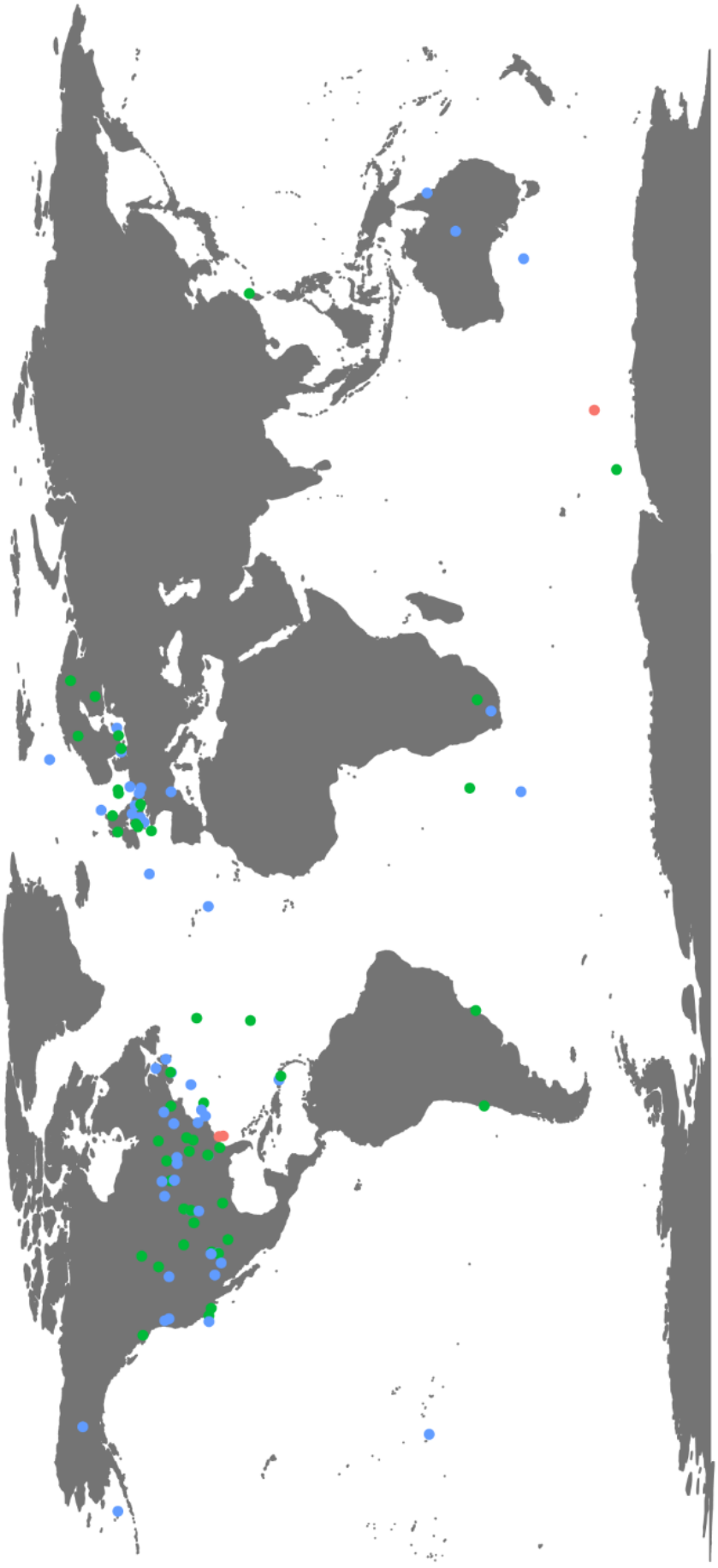


Figure 27. The distribution of assemblages used in Chapter 4. Points are the central locations of each assemblages, and colours represent which questions they were used in. Blue points were only used in the dominance structure questions (Q1 and Q2) and the turnover question (Q3). Green points were used in the dominance structure and turnover questions, and the dominant species body size question (Q4). The red points represent the four fish assemblages used in all the analyses, including the question on declining body size within dominant fish species (Q5).

4.2 Introduction

One of the few universal patterns in ecology is that one or a few very common species dominate assemblages (McGill *et al*., 2007). These numerically dominant species can contribute disproportionately to ecosystem services, so even a small change in their relative or absolute abundance could have large consequences for ecosystem functioning and sustainability (Gaston and Fuller, 2008; Lohbeck *et al*., 2016; Winfree *et al*., 2015). Because increasing dominance is linked closely to decreasing diversity, a greater understanding of how and why the dominance structure is changing is necessary for quantifying and predicting ecosystem change under increasing anthropogenic pressure. The abundance of the most dominant species, and consequently the dominance structure, could change if certain taxa are favoured (or dis-favoured) in human-dominated landscapes. For example, dominant generalist species may acquire an increased competitive advantage over less abundant species in response to environmental change (Kardol *et al*., 2010; Revermann *et al*., 2016; Walker *et al*., 2006). An important question is whether this competitive advantage of dominant species is leading to a systematic increase in dominance globally. Alternatively, abundances of dominant species may be closely linked to changes in assemblage size. In this case, changes in the abundance of dominant species would not signal shifts in the dominance structure, and so not suggest changes in relative competitive ability of rare and common species.

The abundance of a dominant species is not, however, the only factor of interest when assessing change within assemblages. Elucidating identity-based shifts in assemblages in is a key challenge in building a predictive framework of biodiversity change in a rapidly changing world (Hillebrand *et al*., 2017). The abundance and identity of a species combine to shape its influence on ecosystem functioning (Cardinale *et al*., 2012). Indeed, the identity of the dominant species is often the main driver in influencing biomass production, community composition and functioning (Massaccesi *et al*., 2015). Changes among dominant species are consequently of great concern for understanding ecosystem functioning. A recent meta-analysis of assemblages globally found evidence for a systematic increase in turnover (Dornelas *et al*., 2014). However, turnover of species identity within assemblages is highly influenced by rare species. It is as yet unclear whether the turnover detected by Dornelas *et al*. (2014) percolates throughout the whole assemblage, and so signifies increasing turnover of dominant species as well as rare species.

Species traits are arguably as important as species identities when studying the effects of assemblage change on ecosystem functioning. A particularly important trait related to the identity of a dominant species is body size. Body size is a key trait to focus on when assessing ecosystem functioning because it is closely linked with many other important life history traits and functions such as metabolic rate

(Brown *et al*., 2004), range size (Brown and Maurer, 1989) and food sources (Brown and Maurer, 1989). As habitats become increasingly disturbed, smaller more r-strategist species are expected to become increasingly dominant (Warwick, 1986). This is because smaller species are less vulnerable to extinction, in part because they often have higher reproductive output (Cardillo, 2003). One potential consequence of increasing anthropogenic pressures is therefore a systematic shift towards smaller dominant species. The slope of the size spectra (i.e. the distribution of species body size within an assemblage) gets steeper in more heavily impacted assemblages, meaning there are fewer large individuals and more smaller ones (Petchey and Belgrano, 2010). Shrinking body size is also a reaction to climate change (Sheridan and Bickford, 2011), particularly in aquatic systems (Daufresne *et al*., 2009). As such, there could be shifts in ecosystem functioning irrespective of changes in the dominance structure. Consequently, an essential question to address when assessing changes among dominant species is whether there is a systematic shift towards smaller species globally.

Because of its potential importance for understanding the causes and consequences of ecosystem change, there is a need for more knowledge of how dominance is changing under increasing anthropogenic pressures. In this chapter, I address this knowledge gap by analysing trends in the structure and identify of dominant species. I focus on dominance quantified in terms of numerical abundance not biomass, because this measurement of abundance (counting) is more comparable across taxa. The quantification method for numerical abundance is always counts. For biomass, on the other hand, quantification methods vary significantly between and within taxonomic groups. For example, the biomass of fish might be estimated in terms of body length (mm) or body mass (g). Plant biomass might be estimated in terms of above ground biomass, above and below ground biomass, or cover (m^2).

In this chapter I ask five related questions regarding systematic shifts in dominance:

1. *Is there evidence of systematic temporal changes in the dominance structure within assemblages over time?*

   I expect an increase in dominance, because those abundant generalist species that can adapt to changing conditions will be increasingly outcompeting other less abundant species (Kardol *et al*., 2010; Revermann *et al*., 2016; Walker *et al*., 2006).

2. *Does dominance change as a by-product of shifts in assemblage size?*

   If dominance is regulated (i.e. does not change directionally) by the same processes that regulate abundance, any changes in the abundance of the dominant species, although not necessarily identity, will be in proportion to change in assemblage size. In this scenario, absolute dominance will track changes in assemblage size, but relative dominance will not. On

the other hand, a shift in the relative abundance of the dominant taxon (with or without change in absolute dominance) would suggest that assemblages are being restructured as they change in size.

3. *Is there more turnover among dominant species than we would expect by chance?*
   Natural assemblages are not static, so a certain amount of turnover in who is dominant is to be expected. However, a recent analysis focusing on species richness change found evidence of systematic increases in turnover within assemblages (Dornelas *et al*., 2014). An important question is whether this increasing turnover is taking place across all abundance classes, or whether it is predominantly a phenomenon of transient rare species. To address this question, I compare the number of dominant species in each assemblage against the predictions of a null model.

4. *Are smaller species replacing larger dominant species, leading to decreasing dominant body size?*
   This question only focuses on vertebrate species because invertebrate taxa vary far more in terms of life history traits (i.e. size, presence or not of exoskeletons, growth rates) than vertebrates. This increased variation would have introduced additional scatter to already noisy data. I expect that smaller dominant species will be increasingly replacing larger dominant species over time, because smaller species tend to be more numerous and so less vulnerable to anthropogenic disturbance (Cardillo, 2003).

5. *Are dominant species undergoing within species body size declines?*
   The body size distributions of species at a specific location and time can vary substantially from general species descriptions, particularly for taxa like fish that continue growing past age of first reproduction. Species descriptions give mean or maximum values for taxa, but do not reflect natural variations in body size between locations and years. To aid in the interpretation of body size results, and specifically to consider the validity of the average body size measurements from outside sources, it is necessary to check for declining body sizes within species populations as well as between species populations. For this section of my analysis, I focused only on fish because fish body sizes can vary substantially within and between species. There is also much evidence from the literature that fish species are generally undergoing declining body size (e.g. Daufresne *et al*., 2009; Duplisea and Castonguay, 2006). I therefore ask whether the fish species that are at some point dominant are undergoing within-species

declines in body size. As with the analysis of species level change in dominant body size, I expect populations to be declining in body size because fish with smaller body size have an advantage in warming conditions (Daufresne *et al*., 2009). In addition, fishing activities focus on larger individuals, which means smaller individuals are less likely to be removed from the assemblage (Duplisea and Castonguay, 2006). I expect that this analysis will detect a greater decrease in body size than the externally derived body size analysis, because body size declines within species populations are likely to contribute to body size declines above and beyond the effects of smaller species replacing larger dominant species.

4.3 Methods

4.3.1 Data source and preparation

For this chapter, I used the BioTIME database of monitored local species assemblages (Dornelas *et al*., 2018). This database contains additional time series from that of *Chapter 3*'s analysis, because data were continuously added to the database over the period of my study. To avoid the effects of too few sampling years, I selected only the 121 assemblages that had at least 10 sample years (**Figure 27**). I also chose only assemblages where abundance had been quantified as numbers of individuals or in density of individuals. Of these assemblages, 62 where marine, 55 were terrestrial, and 11 were freshwater. Further details on which assemblages I used can be found in **Appendix Table 3**.

To exclude within-year variation I summed the abundance of each species each year within each assemblage. I then applied sample-based rarefaction (**Figure 28**; Dornelas *et al.*, 2014) to each assemblage to account for sampling differences. Analysis was undertaken in R (R Core Team, 2018).

4.3.2 Dominance structure

I defined the dominant species as the species that was most numerically abundant in a given year. Note that I am interested only in the abundance of this species, not its identity (the identity of the dominant can change between years). Where two species were equally dominant in a year, I selected the first species listed in the dataset. There were 117 years across 22 assemblages where there was more than one species dominant. In 49 of these cases there were 2 species dominant. The maximum number of species dominant within a single assemblage was 120 in Study 44. In each year, I computed the following values: assemblage size - the summed abundance of all species in the assemblage; absolute abundance of the dominant - the number of individuals recorded for the dominant species; relative abundance of the dominant - absolute abundance of the dominant species divided by assemblage size.

To assess whether there was a systematic increase in dominance, I constructed two mixed models using the R package lme4 (Bates *et al*., 2015). For the absolute dominance model, $\log_2$ abundance was regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope (**Equation 4**). I used $\log_2$ abundance because there is a large amount of variation in species population sizes. By logging the abundance data, I account for the differences between assemblages by focusing on proportional change. Similarly, for relative dominance, the percentage of the overall assemblage size taken up by the dominant species each year was regressed against mean-centred year, with assemblage identity included as a random effect with varying intercept and slope. I then calculated an overall rate of change for each model, as well as slopes of absolute and relative dominance change within each assemblage.

Equation 4. The mixed model used to calculate rates of change of dominance in each assemblage. Model fit plots are in (a) **Appendix Figure 11** and (b) **Appendix Figure 12**.

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

η_i is dominant abundance for value $_i$, quantified in terms of either a) $\log_2$ abundance for absolute dominance model or b) relative (percentage) dominance for the relative dominance model

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is residual error

To explore whether observed trends in dominance differ from what would be expected by chance (assuming realistic population dynamics), I next employed a cyclical shift null model (*sensu* Hallett *et al*., 2016); **Figure 29**). The purpose of the null model was to provide an estimate of dominance variability due to random fluctuations. To do this, I shuffled every assemblage 1000 times using the random shift permutation and calculated its rate of change in both D_a and D_r on each run using the same mixed models as for the observed data above; this gave a null distribution of 1000 slopes per assemblage. I then asked where the observed slope of dominance change lay relative to the null distribution for that metric and assemblage; observed values below the 2.5% or above the 97.5% quantile were assumed to exhibit a significant shift. I recognise that this analysis does not take account of multiple testing, but note that any correction for this would have the effect of decreasing the number of studies departing from the null expectation.

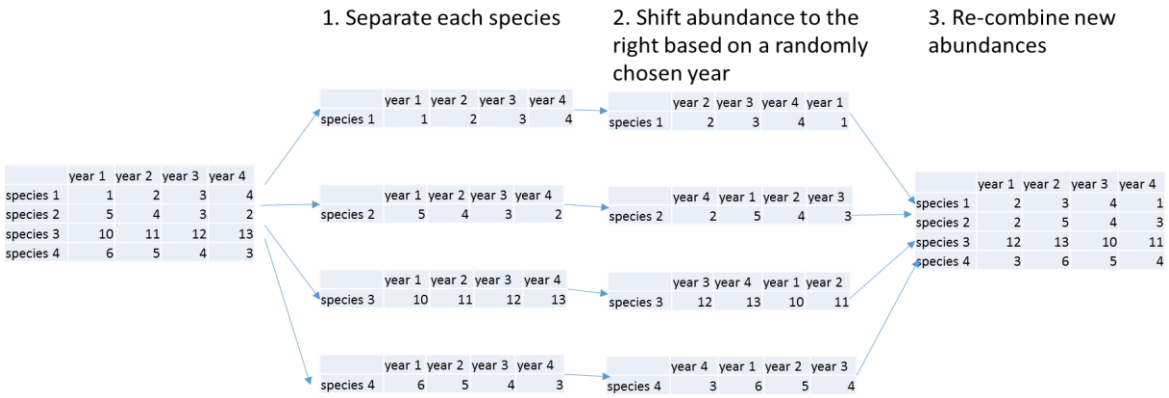


Figure 29. The structure of the cyclical permutation null model, as applied to each assemblage individually. The model is based on the concept of a cyclical permutation model as described in (Hallett *et al*., 2016). Each iteration of the null model entails randomly shifting the abundances of each species within each assemblage, and then applying the mixed model analysis. The whole process is then repeated another 999 times, giving an output of 1000 rates of change for each assemblage for each metric of change.

To test whether there are patterns of dominance change within the general trend, I tested for a significant difference between taxa or realms, and I tested for a pattern's scaling with study length. To check for the effect of taxa and realm tests by plotting slopes of change, split by taxonomic group or realm. In addition, I tested whether an interaction effect of either taxa or realm was significant when added to **Equation 4**. For the effects of scale, I plotted the scores of the null model comparison for relative and absolute dominance against the number of sampling years.

To assess to what extent changes in assemblage size drive changes in dominant species abundance, I tested for regulation of dominance structure. I did this by comparing how changes in relative and absolute dominance related to changes in assemblage size (**Figure 30**). If absolute, but not relative, dominance tracked changes in assemblage size then the dominance structure is maintained under changing conditions. Dominant species populations in this case increase or decrease proportionately to other species within the assemblage.

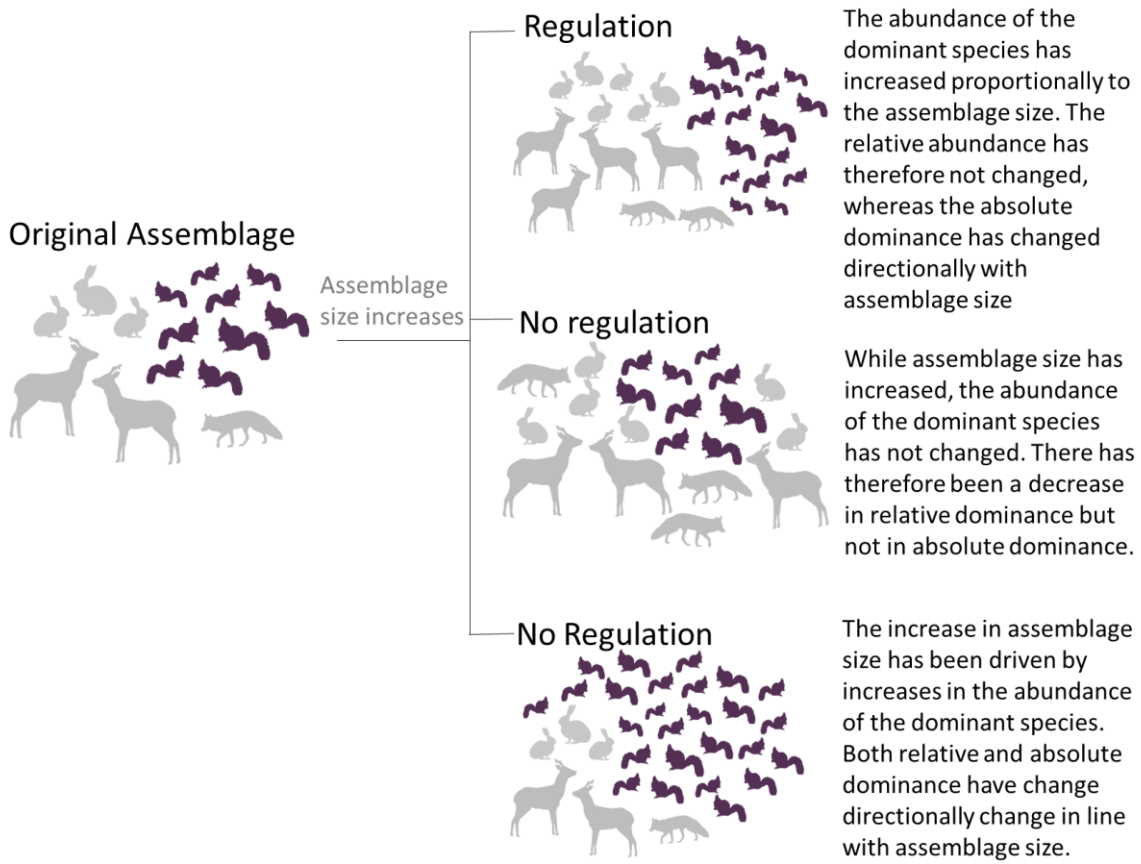


Figure 30. An illustration of how different combinations of relative and absolute dominance changing with assemblage size provide information about the prevalence of dominance structural regulation. There are different ways in which relative and absolute dominance can change under changing assemblage size. In this example, an assemblage of mammals increases. If there is regulation then relative dominance will not change, whereas absolute dominance will. Other combinations of relative and absolute change, relative dominance increasing but absolute dominance not changing, or both relative and absolute dominance changing, indicate no regulation of the dominance structure.

To test for dominance regulation, I first estimated rates of change of assemblage size using a mixed model of $\log_2$ assemblage size regressed against mean-centred year, with assemblage identity included as a random effect with varying intercept and slope (**Equation 5**). I then used model fitting to assess whether including assemblage size change as a fixed effect that interacts with mean-centred year (**Equation 6**) improved model fit in either the absolute or relative dominance models.

I also used the Pearson's Correlation test using the *cor.test* R function to assess the relationship between Z scores of the assemblage size model and the two dominance variables, as calculated from the null model results.

Equation 5. The mixed model calculating rates of change of assemblage size for each assemblage. The slope outputs of this model ($\beta + S_n$) incorporated into **Equation 6** as l_r. Model fit in **Appendix Figure 13**.

$$z_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

z_i is $\log_2$ assemblage size

x_i is the mean-centred year for value $_i$ from dataset

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is residual error

Equation 6. The mixed model that includes an interaction effect of mean-centred year against assemblage size change. Model fit in a) **Appendix Figure 14** and b) **Appendix Figure 15**.

$$\eta_i = \alpha + \beta x_i + m_r l_r + d(x_i + l_r) + b_j + S_j x_i + \epsilon_i$$

η_i is for a) $\log_2$ absolute dominance for value $_i$ and for b) it is the relative dominance for value $_i$

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the overall slope for mean-centred year x

l_r is the value of the fixed effect $_r$ (change in assemblage size of study j for value i)

m_r is the overall slope for change in assemblage size l

$d(x_i + l_i)$ is the interaction between mean-centred year and assemblage size

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is residual error

4.3.2 Turnover

To assess whether there is an increase in the rate at which dominant species are being replaced in the timeseries, I compared the empirical number of dominant species in each assemblage to the results of the cyclical null model used in the dominance structure analysis (**Figure 31**). For each iteration of the null model, I counted the number of dominant species in that assemblage. To assess whether there is greater turnover in the number of dominant species then would be expected by chance, I assessed how often the empirical results fall outside of the 95% quantile range of the null model results.

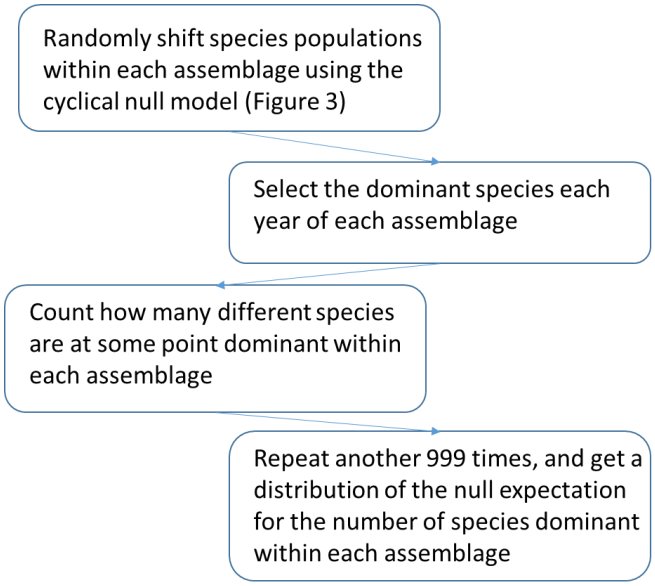


Figure 31. A flow diagram of the workflow of the null model assessing numbers of rare species that are dominant within assemblages

4.3.3 Body size

The BioTIME database does not contain data on body size for most of the datasets, so I sourced body size data from external databases. I focused on fish, mammals, birds and amphibians because the data required are accessible for these taxa from online databases (**Table 10**). Body size quantification methods vary from length to mass measurements, and mean to maximum size, depending on what measurements are available for each taxon. To include the body size data in my analysis, I first selected the dominant species each year of each assemblage. After cleaning and updating taxonomic names, I combined the data on which species are dominant each year with the body size data to get the body size of each dominant species each year. I was not able to extract dominant species in cases where species names were provided only in shorthand in the BioTIME database. I also removed studies that do not experience changes in identity of the dominant species during the study period. For this analysis, I therefore used a subset of 56 studies (**Appendix Table 3**).

Table 10. The databases where dominant species body size data was sourced, along with the measurement of body size used. Where multiple values were given, for instance a range of values or different values for males/females or different areas, a mean of all values given was used.

Taxa	Measurement	Database	link
Mammal	Mean weight (g)	PanTHERIA	http://esapubs.org/archive/ecol/E090/184/metadata.htm
Bird	Mean length (mm)	Handbook of the Birds of the World Alive	www.hbw.com
Amphibian	Mean length at first reproduction (mm)	AmphibiaWeb	amphibiaweb.org
Fish	Maximum length (mm)	FishBase	www.fishbase.org

To assess trends in dominant body size, I asked two closely linked questions. Firstly, when there is a change in dominant species identity, is there more often a shift to larger or smaller dominants? Are smaller dominant species increasingly replacing larger dominant species? For this question I quantified the number of times the new dominant species is either smaller, the same size, or larger than the previous dominant species. If small dominant species are increasingly replacing larger dominant species, I expect more occasions where the dominant new species is smaller than was previously the case. To further explore this question, I then looked for a systematic decrease in the size of dominant species by modeling dominant species body size against time. I fitted a random effects mixed model with varying intercept and slope for each assemblage (**Equation 7**). I logged body size values to account for differences in body size between taxa. I also included measurement type (mass or length) as an additional fixed effect in this model to account for the different body size quantification metrics.

Equation 7. The mixed model regressing $\log_2$ body size of dominant species, and including an interaction effect of mean-centred year against body size metric type. Model fit in **Appendix Figure 16**.

$$\eta_i = \alpha + \beta x_i + m_r l_r + d(x_i + l_r) + b_j + S_j x_i + \epsilon_i$$

η_i is the $\log_2$ body size of the dominant species for value i

x_i is the mean-centred year for value i from dataset n

α is the overall intercept

$\beta$is the overall slope for mean-centred year x

l_r is the intercept for the body size metric r

m_r is the overall slope for body size metric r

$d(x_i + l_r)$ is the interaction between mean-centred year and body size metric

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is residual error

To assess declines in body size within populations, I focused on the case study of fish assemblages. I selected the four fish assemblages that contained individual body size (Studies 119, 125, 232 & 252) and extracted a list of all the species that were dominant at least once throughout the assemblage timeseries. Each species was assigned a unique identifier combining the species name and its relevant assemblage. This provided me with 14 populations (each from a different species) across the 4 assemblages. I then extracted mean size values each year for each species within assemblages. With this data, I ran a mixed model of mean body size regressed against mean-centered year, with assemblage/species ID as a random effect (**Equation 8**).

Equation 8. The mixed model calculating rates of change of dominant fish species mean body mass for each assemblage. The random effect refers to an ID value which combines species name and the assemblage it is dominant in. Model fit in **Appendix Figure 17**.

$$z_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

z_i is $\log_2$ dominant species mean body mass

x_i is the mean-centred year for value i from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope values with the random effect j

ϵ_i is residual error

4.4 Results

4.4.1 Dominance structure

I detected no systematic change in either absolute dominance (slope: 0.006, SE: 0.009; **Figure 32A**) or relative dominance (slope: -0.03, SE: -0.05; **Figure 32B**). The analyses with the cyclic shift null model supported this conclusion, because cases of positive and negative change were slightly less balanced for absolute dominance (decrease in dominance relative to the null expectation: 19 (16%) studies; increase: 38 (31%) studies; no change 64 (53%) studies) than for relative dominance (decrease: 50 (41%) studies; increase: 36 (30%) studies; no change: 35 (29%) studies.

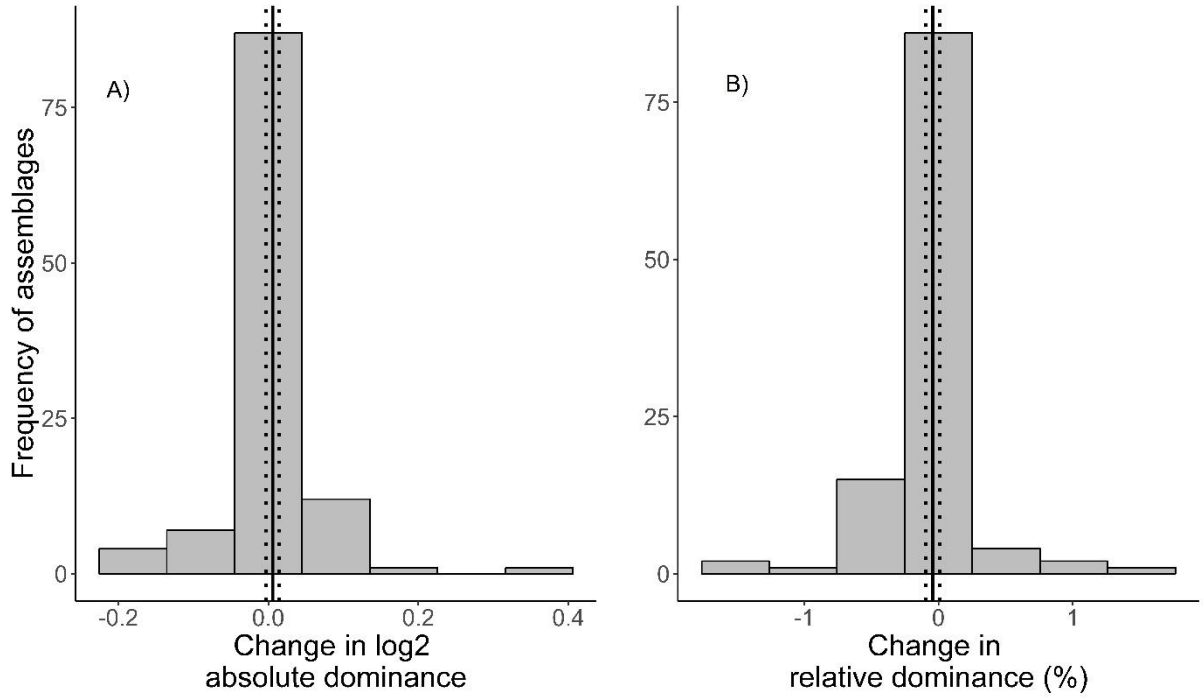


Figure 32. The distribution of rates of change of absolute (A) and relative (B) dominance within assemblages. The solid line represents the overall model slope of change, and the dotted lines represent the standard error around this estimate. In both cases the overall estimate of change is not significantly different from 0.

In line with my results in *Chapter 3*, I detected no systematic change in the assemblage size of studies (slope: 0.003, SE: 0.006; **Figure 33**), but this overall trend was underlain by temporal variation in numerical abundance within and among assemblages. Relative dominance, on average, represents less than 20% of assemblage size in the majority (86) of assemblages (**Figure 34**).

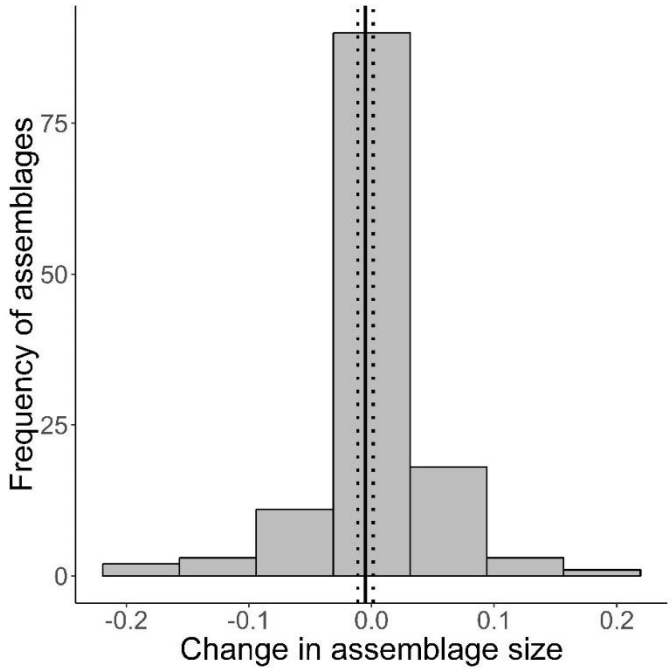


Figure 33. The distribution of rates of change of assemblage size. They are generally centred on 0, no evidence of a systematic change in assemblage size. The solid line represents the overall model slope of change, and the dotted lines represent the standard error around this estimate.

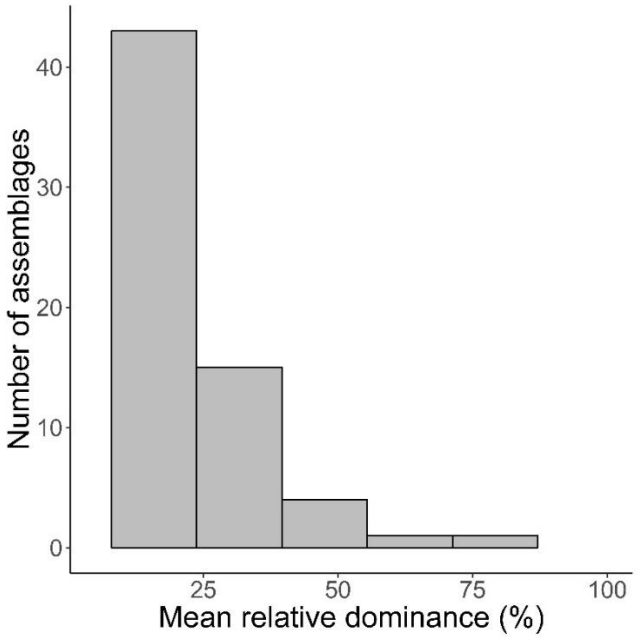


Figure 34. Mean relative dominance of assemblages. In most cases (89 assemblages), the mean relative dominance of dominant species within assemblages was less than 20% of the total assemblage size. Although dominant species are, by definition, more numerous than other species within the assemblages, they do not often contribute extremely high proportions of N.

Most studies with a change in absolute dominance underwent a similar change in assemblage size (Pearson's Correlation: 0.70, p: <0.001, **Figure 35A**). Including rate of change of assemblage size and its interaction with time improved the absolute dominance model's fit (p: < 0.001). In this model, the rate of change of assemblage size interacted significantly with change in absolute dominance over time (p: <0.001), supporting a positive relationship between change in absolute dominance and change in assemblage size.

There was, conversely, a weak negative relationship between changes in assemblage size and changes in relative dominance (Pearson's Correlation: -0.22, p: 0.02, **Figure 35B**). Including rate of change of assemblage size in the relative dominance change model also did not improve model fit (p: 0.19).

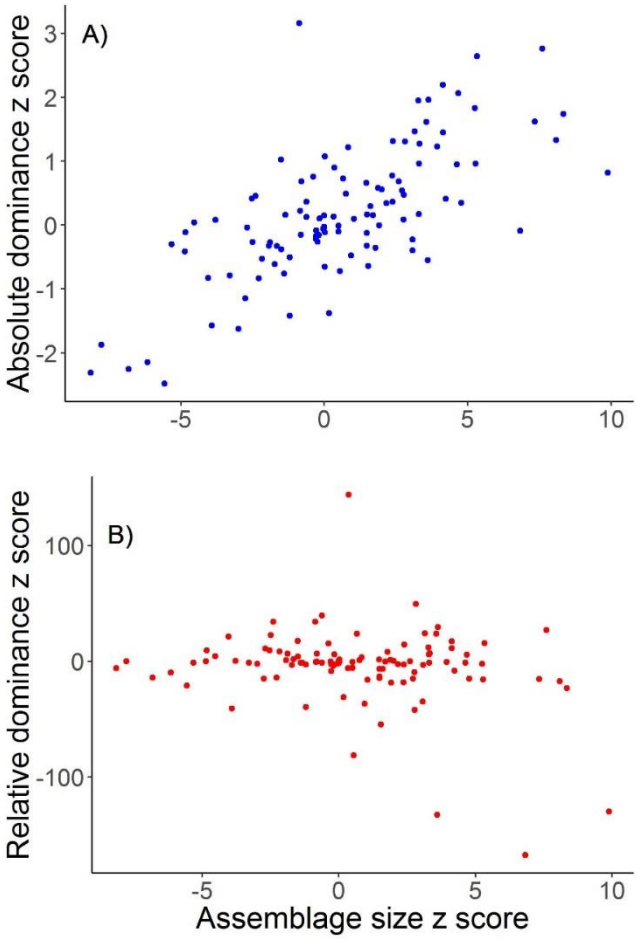


Figure 35. Z scores from the assemblage size change model against both the relative and absolute dominance change models. A positive relationship is evident for absolute dominance but not relative dominance.

There were no significant interaction effects between realms (marine, terrestrial or freshwater) and mean-centred year in the extended mixed models, nor are there any discernible differences in the plotted slopes (**Figure 36**; **Table 11**). This result suggests that there are not significantly different patterns of dominance change between marine, terrestrial and freshwater assemblages. There is some suggestion that absolute dominance might be increasing in reptiles, and relative dominance increasing in reptiles and amphibians (**Figure 37**; **Table 11**), but there are insufficient data to indicate a significant difference. This is supported by the fact that neither an absolute nor a relative dominance model found a significant interaction effect between taxonomic group and mean-centred year (**Table 11**). There was also no directional pattern discernible with increasingly long timeseries (**Figure 38**).

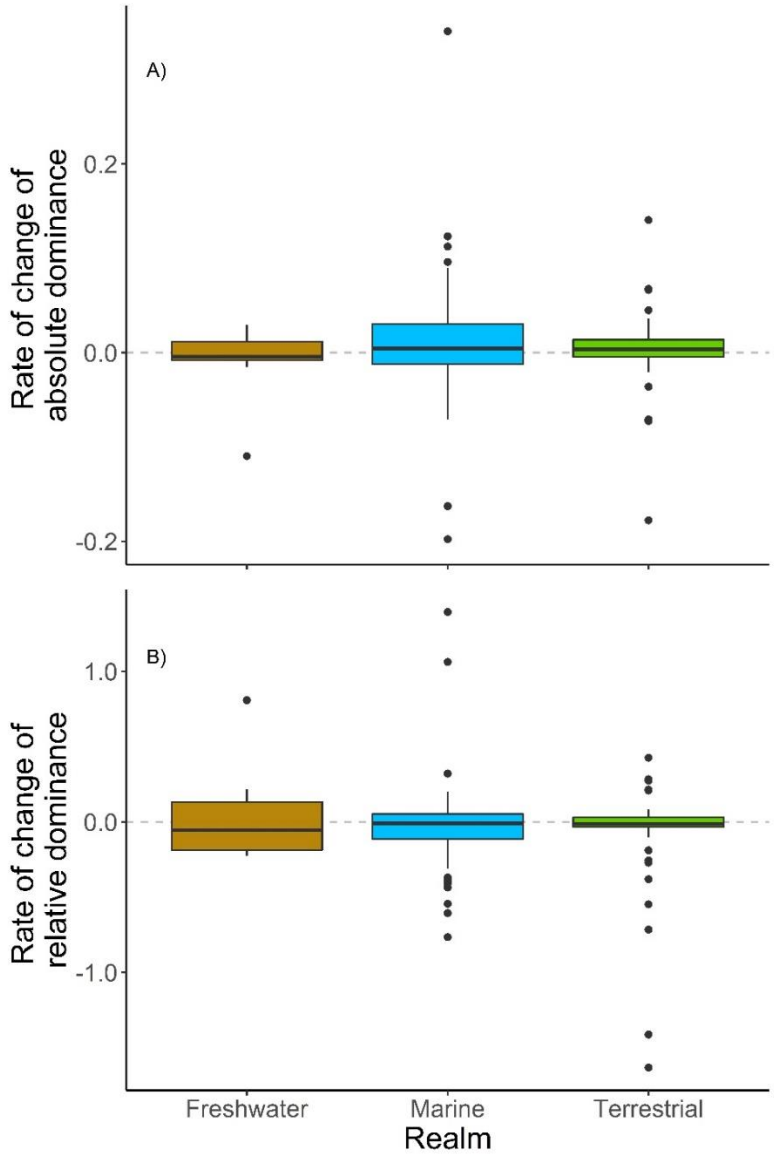


Figure 36. A box plot of changes in absolute A) and relative B) dominance in terrestrial, marine and freshwater ecosystems. There are no clear differences in changes in dominance between the three realms

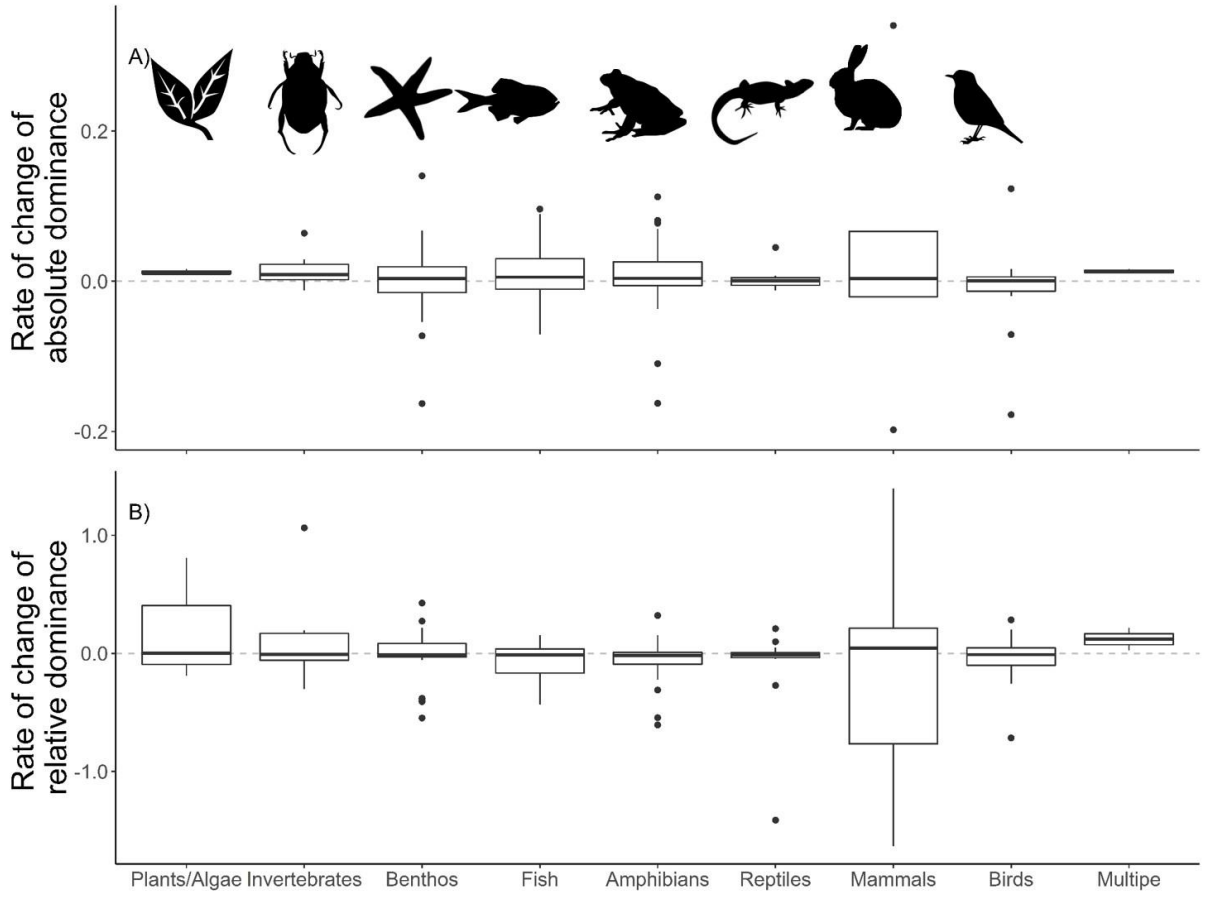


Figure 37. A box plot of changes in absolute A) and relative B) dominance, split by taxonomic groups. Groups were split to different taxonomic levels to reflect amounts of data for each taxon. No clear patterns emerge from splitting slopes of change by taxonomic group.

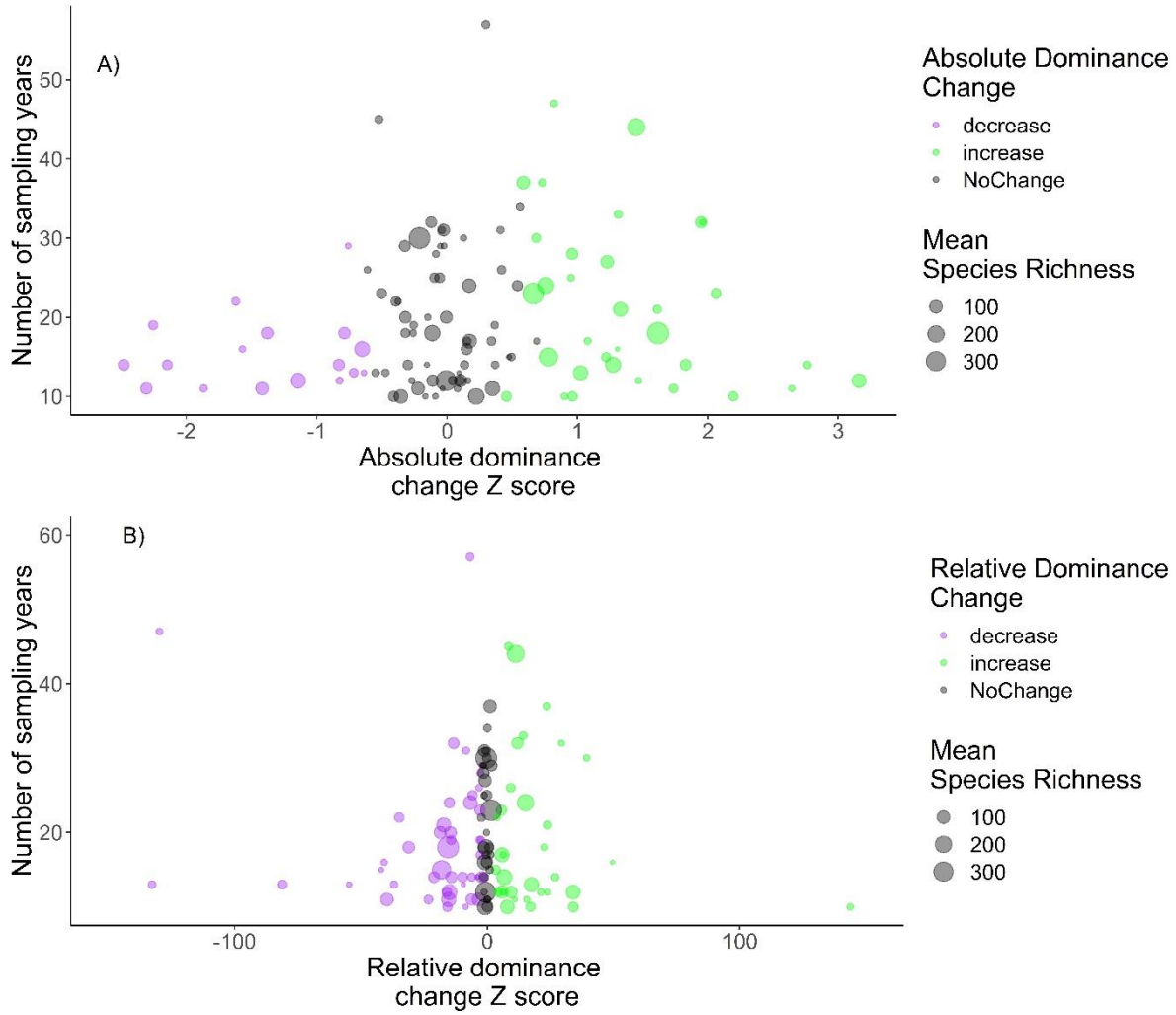


Figure 38. Z scores of A) Absolute Dominance and B) Relative Dominance from the null model plotted against the number of sampling years. Points are coloured based on whether the assemblage they represent displayed a systematic increase (green), decrease (purple) or no change (grey). Points are sized based on the mean species richness of the assemblage, with the largest points having a species richness close to 1000 species. These plots show that assemblages with longer time-periods sampled are not more likely to exhibit change.

Table 11. The AIC values relative to the lowest value and T values of the different mixed model structures used to assess the interaction between dominance change and assemblage size change, realm and taxonomic group. The only interaction effect that was significant (i.e. T value over 2) was the interaction between absolute dominance and assemblage size change. This model also had a substantially lower AIC than the comparable model without assemblage size change. This interaction was therefore used in all subsequent absolute dominance models. The AIC for the absolute dominance model including realm as a fixed effect was lower than the corresponding model without realm, but in this case the interaction effects were not significant.

Dominance Type	Interaction effect	AIC	T value
Absolute	None	200	
	Assemblage Size	32	20
	Realm	0	>2
	Taxa	28	>2
Relative	None	0	
	Assemblage Size	1	>2
	Realm	1	>2
	Taxa	3	>2

4.4.2 Turnover

My results suggest a positive trend in increasing turnover of dominant species (**Figure 39**). Although most cases (69%) show no evidence of a trend in turnover, there are far more assemblages showing increasing turnover (24%) than decreasing turnover (7%).

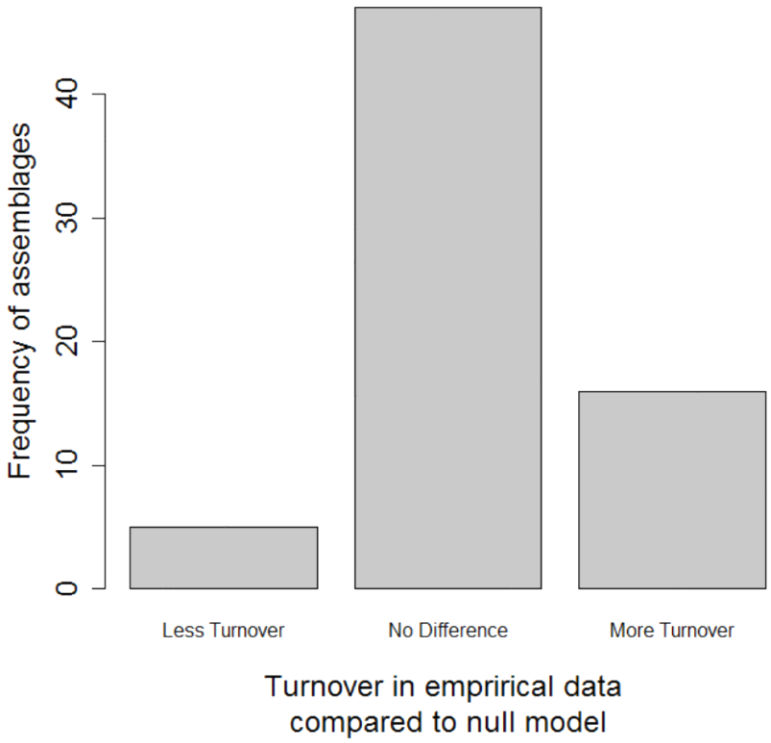


Figure 39. The results of the comparison between empirically documented turnover of dominant species and the null model expectation. Assemblages that have fewer species dominant than the lower 2.5% quantile of the null model have less turnover than expected by chance. Assemblages that have more species dominant than the lower 97.5% quantile of the null model results have more turnover than expected by chance. Any assemblage with a number of dominant species that falls within the expected number according to the null model have no difference. In most cases (47), there is no difference between the number of dominant species in the empirical data vs the null expectation. In cases where there is a notable difference between empirical results and null predictions, there are more cases (16) of increased turnover than decreased turnover (5).

4.4.3 Body size

There were 1144 occasions where the dominant species changed identity within the selected vertebrate assemblages. My analysis of directional shifts in body size provided no evidence that smaller species are generally becoming dominant more often over time (**Figure 40**). In most cases dominant species body size remained constant (62%). When there was a change in body size, it was a decrease in only 18% of the occasions. Body size increased in the remaining 20% of occasions.

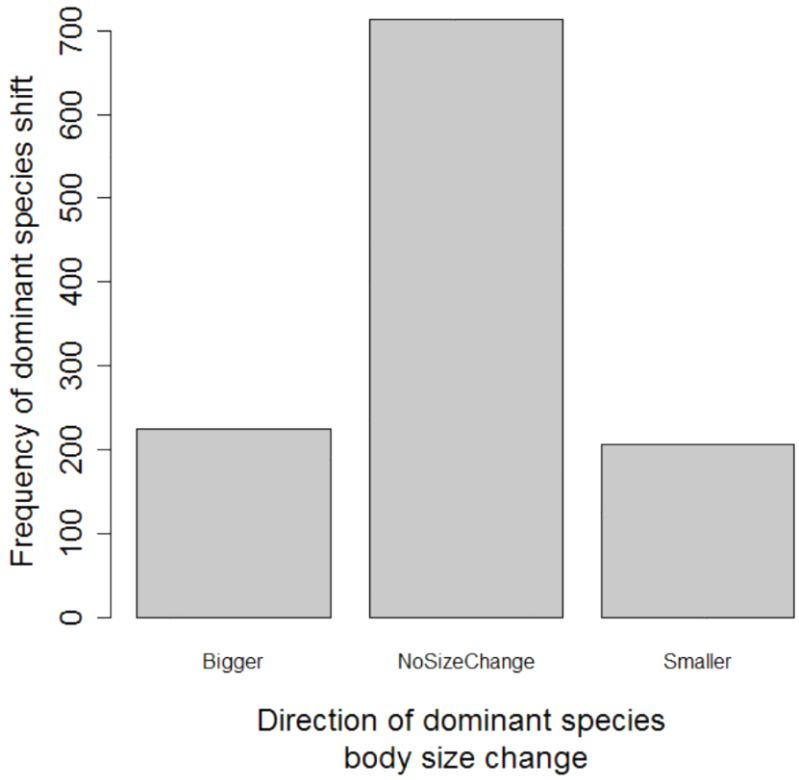


Figure 40. The frequency of direction of change in body size when there is a change in identity of the dominant species. In 713 of the 1144 occasions where dominant species identity changed, there was no corresponding change in body size. Where there is a change in body size, these changes were similarly distributed amongst occasions of increasing body size (225) and decreasing body size (206).

No trend in decreasing body size was detected in the mixed model of dominant vertebrate body size data (slope: -0.00042, SE 0.0019; **Figure 41**), and there was no significant effect of measurement type (T value: -0.737; **Figure 42**).

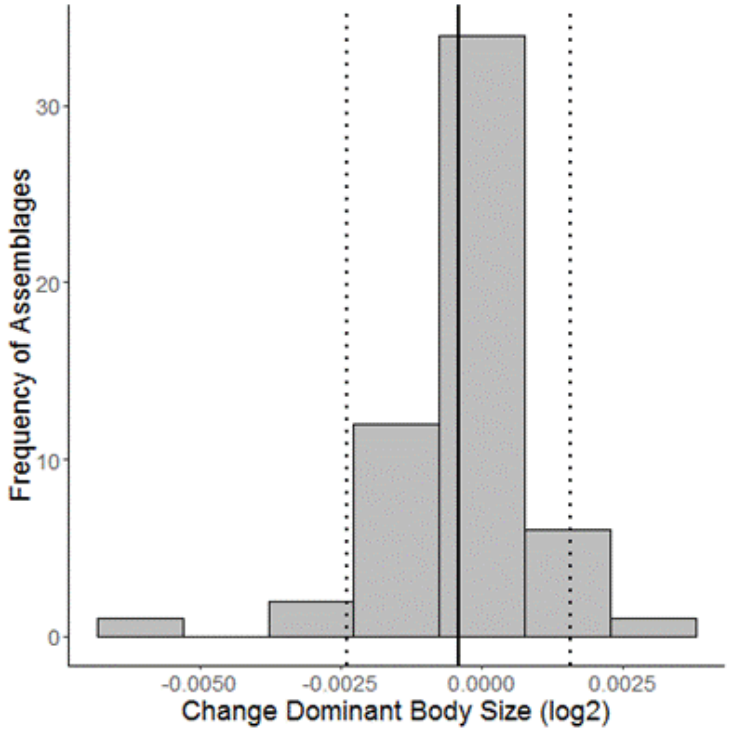


Figure 41. The slopes of change of dominant species body size within assemblages over time. Although there are more increasing slopes than decreasing slopes, this does not translate to a significant systematic increase in the overall model trend. The solid line represents the overall model slope of change, and the dotted lines represent the standard error around this estimate.

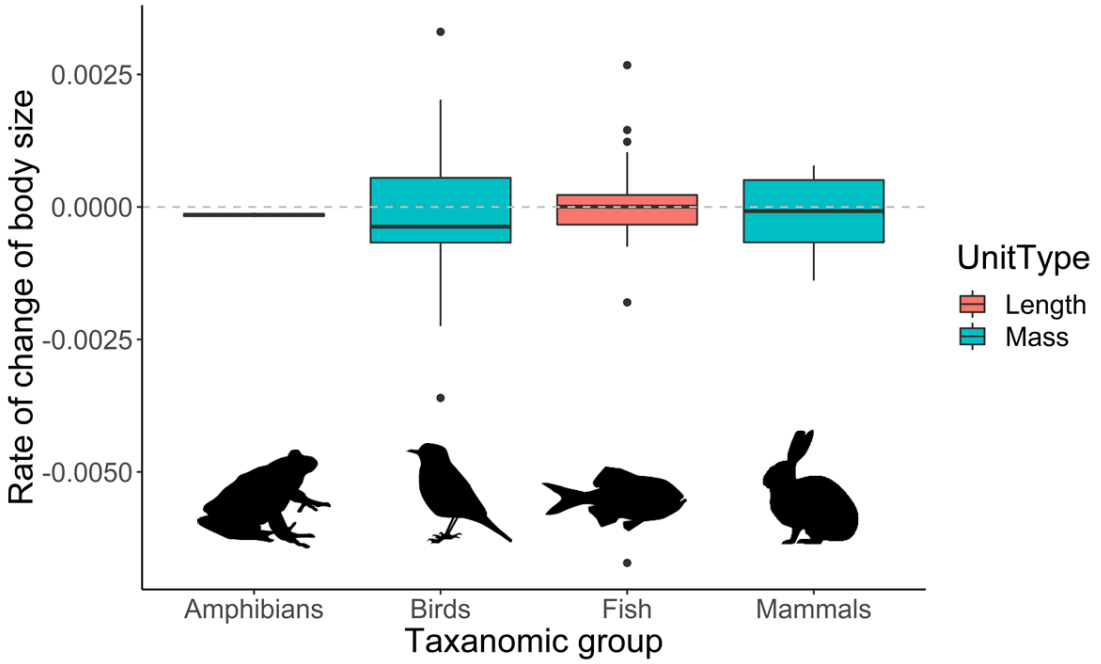


Figure 42. A box plot of slopes of change of dominant species body size, split by taxonomic group. Body size estimates were extracted from external databases and represent species averages. Amphibian and fish body size were quantified in terms of length (mm). Bird and mammal data were quantified in terms of mass (g).

The results of the analysis of within population body size shifts of dominant fish species, where individual fish body mass data was available, found a general decrease in body size (-0.004, SE 0.003). For one of the four fish assemblages there was a significant increase in body size instead (0.055, SE: 0.16), but the majority of populations in the analysis had negative body mass slopes of change (**Figure 43**).

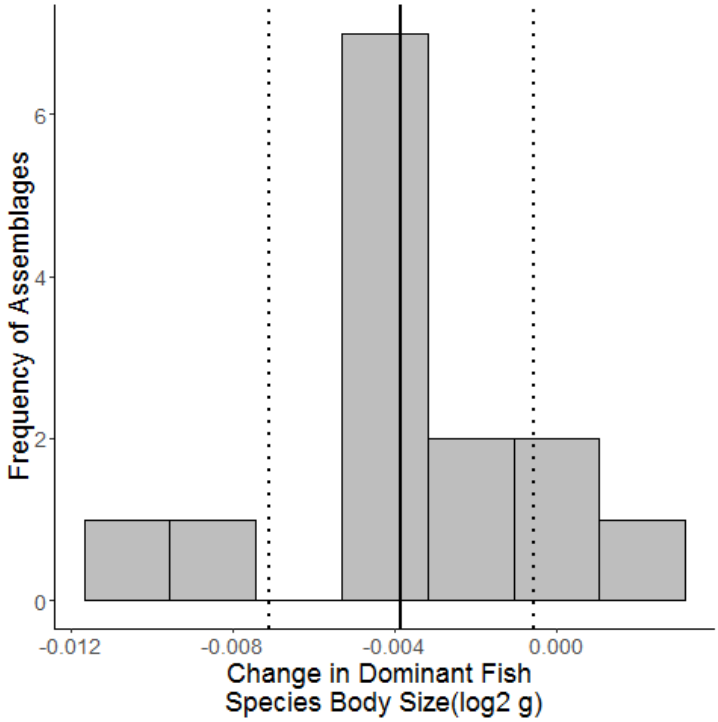


Figure 43. The slopes of change of each population of a dominant fish found in the four fish assemblages that contained body mass data. Most species show declining body size over the study period. The solid line represents the overall model slope of change, and the dotted lines represent the standard error around this estimate.

4.5 Discussion

In this chapter I found no evidence of a systematic increase in dominance, and no evidence for differences between realms or taxonomic groups. However, shifts in dominance were present in some assemblages, and generally tracked changes in overall assemblage size. There was a general increase in turnover of dominant species, but no evidence for a general decrease in dominant species body size. There was, however, evidence for declines in the body size of the dominant fish in assemblages.

4.5.1 Dominance structure

The result that the dominance structure is not changing systematic is contrary to predictions from the literature (Hillebrand *et al*., 2008). Many different external drivers are expected to alter the dominance structure, such as climate change (Kardol *et al*., 2010; Walker *et al*., 2006), pollution (Gray and Mirza, 1979; Hillebrand *et al*., 2007) and land use intensity (Revermann *et al*., 2016), so the lack of detectable change in my data is surprising, and suggests that dominance is being regulated alongside assemblage size and species richness (Gotelli *et al*., 2017). In other words, dominant species continued to account for approximately the same fraction of the assemblage, even when it contracted

or expanded in assemblage size. Thus, there is little support for the idea that common species are increasingly dominating ecosystems. The widespread regulation of dominance across taxa and realms that I detected suggests that common species are not reacting disproportionately to environmental change. Common generalist species are therefore not systematically becoming increasingly successful as habitats are disturbed, nor are dominant species increasingly maintaining assemblage size.

That the dominance structure is generally regulated has implications for species coexistence theories. The dominance structure arises from a combination of stabilizing niche differences and relative fitness differences which are intricately linked to environmental and biological conditions of the assemblage (HilleRisLambers *et al*., 2012). Assemblages that are increasing or decreasing in assemblage size are likely undergoing some form of change in environmental and biological conditions. This driver (or drivers) of change may cause a shift in the fitness differences between species, for example perhaps smaller but more numerous species (Sheridan and Bickford, 2011). Stabilizing niche differences cause species to have lower growth rates when common than when rare, thereby buffering rare species from extinction while stopping abundant species from using all the resources available to the assemblage (Adler *et al*., 2007; Chesson, 2000). Such niche differences may arise from species interactions with predators, resource partitioning or host-specific enemies (HilleRisLambers *et al*., 2012). For example, if a parasite targets a species successfully only when that species is living in high densities, then once that host species reaches a critical density its grow rate will decline. For the dominance structure to be regulated in a scenario where assemblage size is changing, stabilizing niche differences between species are likely remaining unchanged. This suggests that the number and size of realised niches of the species within the modified assemblage are not altered with change in assemblage size (Sheridan and Bickford, 2011).

4.5.2 Turnover

The results of my turnover analysis suggest a general increase in turnover of dominant species. There were noticeably more instances where assemblages had a greater number of species dominant over the timeseries than expected by chance. The identities of dominant species are generally far more stable than that of rare species (Magurran and Henderson, 2003). Consequently, it might be expected that the increasing turnover detected by Dornelas *et al.* (2014) is a result of changes amongst species with very low abundances which likely have low impacts on ecosystem functioning. My results, however, suggest that the increasing turnover within assemblages is not taking place only among the rare species. What is driving the increased turnover is unclear. One potential cause is increased immigration of invasive species. Because they are often generalist species, invasive species can exist in higher abundances than native species. This situation was detected among the breeding birds of

North America, where exotic species were able to reach higher abundances than their native cohabitants (Labra *et al*., 2005). Because it is often the identity, and not the relative abundance, of dominant species that strongly influence ecosystem functioning (Wohlgemuth *et al*., 2016), my results suggest that assemblages may be undergoing changes in ecosystem functioning despite the regulation of the dominance structure.

4.5.3 Body size

I found little evidence that the increasing turnover of dominant species detected in my analysis is leading to a shift in ecosystem functioning with respect to body size. When a new species became dominant in an assemblage, it was not more likely to be a smaller species than the previous dominant species (**Figure 39**). Smaller species are therefore not generally replacing larger dominant species. This result is supported by the lack of a systematic decrease in average dominant species size over time (**Figure 41**). On one hand, this result may reflect the fact that my timeseries are all relatively short (decadal time scale), whereas shifts in body size distributions can take centuries or more to be noticeable (Lotze *et al*., 2006). Most of my datasets are also from temperate northern hemisphere assemblages that have already been heavily modified by humans for many centuries. Replacement of large dominant species by smaller dominant species due to anthropogenic pressures may therefore already have taken place by the time my timeseries begin. On the other hand, the relatively short length of the datasets cannot explain all the lack of decreasing body size. Many species, such as the common toad *Bufo bufo* (Reading, 2007), British passerine birds (Yom-Tov *et al*., 2006) and red deer *Cervus elaphus* (Post *et al*., 1997), have undergone noticeable decreases in body size over decadal time scales as a reaction to climate change.

Another factor possibly contributing to the lack of declining body size among dominant species is the use of species-level average body size data extracted from external sources. Body size can be quantified in many ways, i.e. species averages or individual size spectra. Terrestrial analyses have historically focused on taxonomically defined body size, whereas marine analyses focused on size classes and individual body size (Yvon-Durocher *et al*., 2011). The differences between mass- and length-based averages are unlikely to play an influential role in influencing the results, because this was not a significant factor in the model. There is, however, a potential issue with my use of the extracted species level body size averages. Because most of the assemblages in the BioTIME database do not contain individual body size data, I was unable to include the exact body size of the population of species in questions. Instead, I assume that all species included in the analysis are well represented by the body size averages provided by the external databases. This may hold true for species that do not continue growing indefinably, such as mammals, but may be less accurate for taxa like fish where

adult body size can vary significantly. Species descriptions give mean or maximum values for a taxon, but do not reflect natural variations in body size between locations and years. It may be that decreasing body size is expressed in terms of decreases within species instead of replacement by smaller species. Such a decrease in body size would not be detected by an analysis, like mine, that uses species average values from external sources.

The influence of the problem of species' average body size values is illustrated in the case of the fish datasets. The difference between the results of the extracted fish body size data analysis in comparison to the population-level body size analysis is marked. In the first case, the result suggests that dominant fish are not declining in body size, because smaller dominant species are not replacing larger dominant species. This result is contrary to consensus in the literature, where pervasive fish body size declines have been noted across assemblages due to overharvesting (*i.e*. Duplisea & Castonguay 2006) and climate change (Daufresne *et al*., 2009). On the other hand, there is clear evidence that dominant fish species are declining in body size when the mean of the body size distribution each year is calculated directly from fish biomass and abundance data (**Figure 42**). My analysis using externally-sourced fish body size data therefore overlooked any declines in body size within dominant species populations. This result suggests caution when including and interpreting externally sourced species average body size data in analyses searching for functional shifts, because such analyses may miss vital signals of shifts in population size structure.

4.5.4. Conclusion

In this chapter, I found no evidence for the predicted widespread shifts in the dominance structure. Even when there were shifts in the abundance of dominant species, these shifts generally tracked overall assemblage size. However, the regulation of the dominance structure I detected does not preclude substantial changes in assemblages in response to anthropogenic pressures. An important question not addressed in this chapter is how aspects of assemblages other than dominant species are changing. For example, assemblages contain many rare species, and these species are very vulnerable to change due to their small population sizes (Pimm *et al*., 1988). To achieve a more complete understanding of how assemblages are changing, further analysis on changes amongst the less abundant species is needed (*Chapter 5*).

Chapter 5

Increased immigration of rare species into assemblages

5.1 Abstract

As pressures on biodiversity increase, a better understanding of how assemblages are changing is needed. Rare species, defined here as those that have locally low abundance, are potentially sensitive to such change. Here I show that the number of rare species within assemblages is increasing on average across systems. This may arise in two ways: species already present in the assemblage may decrease in abundance without going extinct, or additional species may enter the assemblage in low numbers. By linking change in the number of rare species with change in assemblage species richness, and estimating numbers of rare species immigrating or going locally extinct within assemblages, I find evidence that increasing immigration is driving the detected increase in numbers of rare species. I therefore find clear evidence of measurable changes in the structure of assemblages in the recent past. Furthermore, my results underline the importance of quantifying key aspects of community structure, alongside species richness, when investigating biodiversity change.

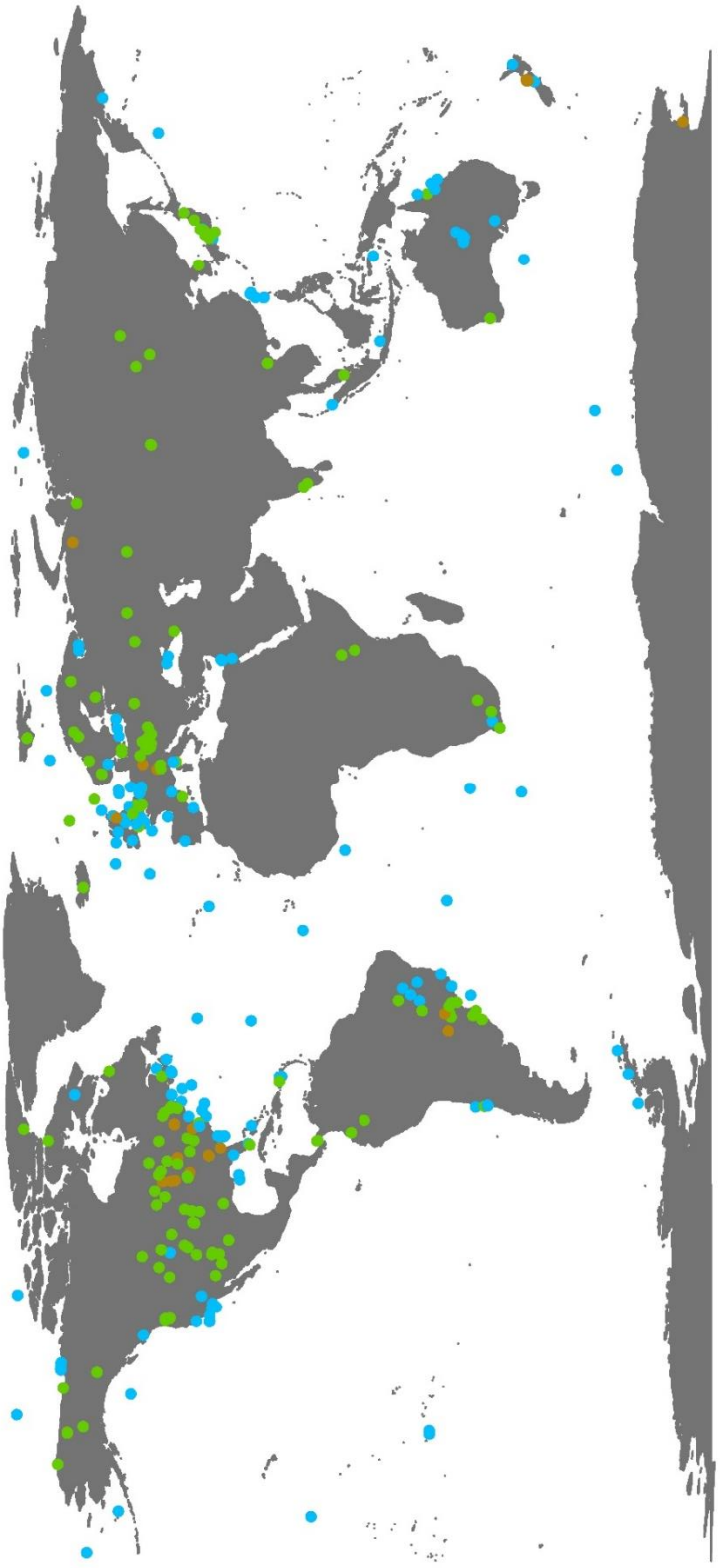


Figure 44. The distribution of assemblages used in *Chapter 5*. Points are the central locations of each assemblages, and colours represent the realm of the assemblage. Blue points represent marine assemblages, green points represent terrestrial assemblages, and orange points represent terrestrial points. Some marine points have central locations in terrestrial areas because the data are spread widely in the seas around those points.

5.2 Introduction

Rare species, defined in this analysis as species present within assemblages in low abundances, make up the majority of biodiversity because most species are rare throughout most of their range. In fact, one of the few consistent patterns across assemblages is that they contain few common species and many rare species, meaning rare species contribute considerably towards species richness (Fisher et al., 1943; McGill et al., 2007; Preston, 1948). Despite being locally uncommon, rare species can also contribute significantly to ecosystem functioning (Lyons et al., 2005). For example, rare species disproportionally increase the potential diversity of functional traits within assemblages (Mouillot et al., 2013), and can increase multifunctionality across trophic levels and land use (Soliveres et al., 2016). Here, I assess how the number of rare species in assemblages is changing on average, and suggest the main mechanisms driving any detected changes.

Rare species are particularly sensitive to change due to their small population numbers (Pimm et al., 1988). As such, low population sizes have become a criterion for assessing extinction risk (IUCN, 2001). Because of this increased risk, rare species receive priority status for focused conservation efforts (Gauthier et al., 2010). Because rare species make up a high proportion of assemblage species lists, and are potentially very sensitive to change, a better understanding of how the number rare species within assemblages is changing will help elucidate patterns of recent biodiversity change.

Pressures on biodiversity are increasing at an alarming rate, and show no sign of abating (Tilman et al., 2017). In many cases, species population abundances are consequently decreasing (Diaz et al., 2019). If population declines amongst the more abundant species are leading to more species declining to rare status, then population declines are likely to lead to more rare species being present within assemblages. This is especially true if extinction debt (Tilman et al., 1994) leads to few extinctions in the short term despite population declines.

An alternative, or perhaps additional, driver of increasing rarity is an increase in net immigration into assemblages. In this case, if more species are immigrating into new areas in low abundances than there are rare species undergoing local extinction, then the net number of rare species will increase.

How rarity is changing across assemblages may also vary systematically between realms, particularly if increased immigration is strongly influencing rarity, because mobility is generally higher in marine systems than terrestrial and freshwater systems. In addition, the pressures facing potential migrants differ by latitude, with more species expected to be leaving equatorial tropical areas and entering temperate areas as species shift away from the equator (Hickling et al. 2006). Another potential

influence of trends in rare species is the spatial grain of the assemblages in questions, because meta-community dynamics and detection of rare species are sensitive to spatial scale.

In this paper, I firstly set out to test the expectation that there is a general increase in the number of rare species within assemblages, and whether there are detectable differences in trends across different realms, spatial scales or latitudinal bands. Secondly, to distinguish between the two alternative explanations for increasing rarity, I then ask how any detected increases in rarity relates to changes in species richness within assemblages. Under the scenario that declining populations are predominantly driving increasing rarity, there should be no corresponding increase in species richness (**Figure 45B**). Under the alternative scenario that increasing immigration is leading to increasing rarity, on the other hand, species richness should increase with increasing rarity as the immigrating rare species drive up species richness (**Figure 45C**). Thirdly, to further assess the net balance of immigration to local extinction of rare species, I tested the assumption that there were more immigration events than extinction events amongst rare species. If the increasing immigration scenario (**Figure 45C**) was driving increasing rarity, then I expected more rare species to be immigrating than going locally extinct. In this case, species richness will increase with increasing numbers of rare species, assuming already present species are not lost more quickly than new species are gained.

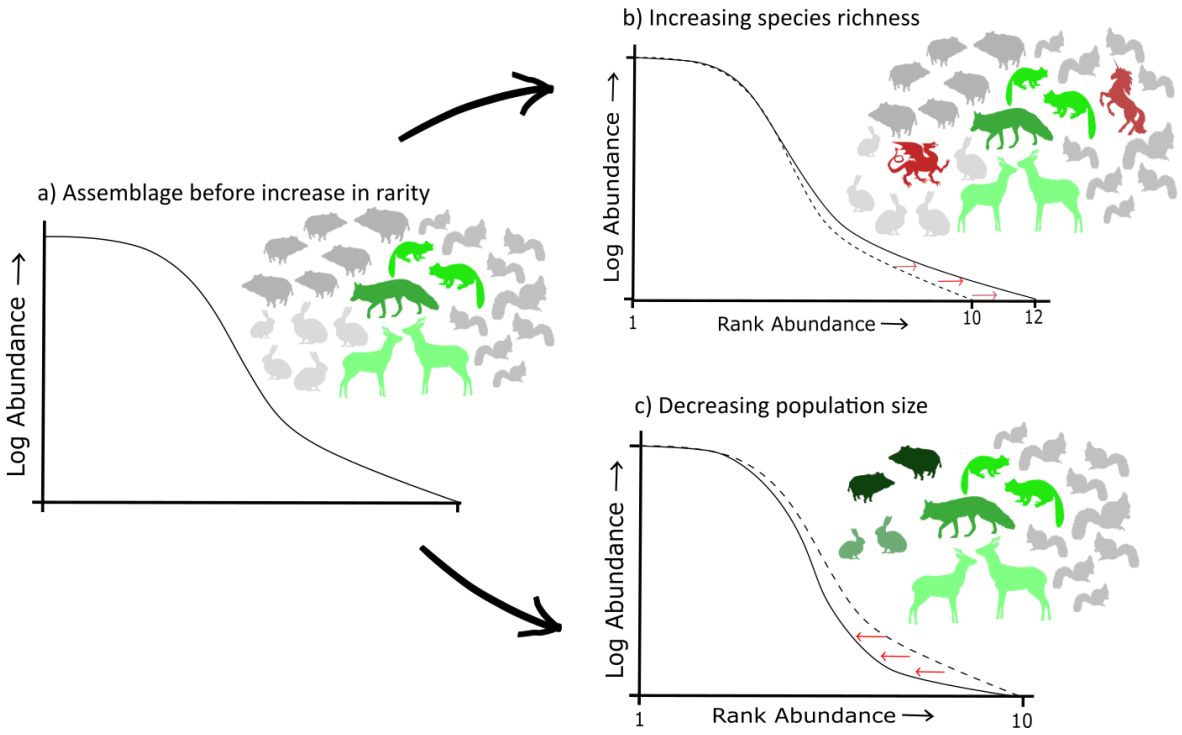


Figure 45. Conceptual framework of how shifts in numbers of rare species may relate to species richness change. I illustrate my example using increasing rarity because this is my prediction. Plot (a) shows the shape of the rank abundance curve before the assemblage undergoes an increase in numbers of rare species. Plot (b) is the change in the shape of the rank abundance curve if the increase in numbers of rare species is driven by more species entering the assemblage at low abundances. These species shift the rank abundance curve to the right as species richness increases but the abundances of the species already in the assemblage do not change. In plot (c) is the alternative relationship between species richness and increasing rarity. In this case increasing rarity is riven by decreasing abundance of species within the assemblage, not by more rare species entering the assemblage. Species richness is consequently unchanged, despite a shift to the left in the rank abundance distribution.

5.3 Methods

5.3.1 Data source and preparation

For this analysis I used a subset of 101 assemblage time series from the BioTIME database (Dornelas *et al*., 2018) that contained at least 10 years of monitoring data and numerical abundance count data (see **Appendix Table 4** for full list). This list includes additional data not included in the *Chapter 3* and *4* analyses, as more studies were added to the BioTIME database in between my undertaking these analyses. These assemblages included 42 marine, 49 terrestrial, and 10 freshwater assemblages, and were distributed across the globe (**Figure 44**). Various taxa were represented, including plants, fish, mammals and invertebrates.

As with *Chapters 3* & *4*, data underwent sample-based rarefaction to account for variation in sampling effort before any analysis took place (*sensu* Dornelas *et al*., 2014). For studies with multiple samples per year, I removed the effects of seasonality by summing the abundance of each species in each year. Analysis was undertaken in R (R Core Team, 2018).

5.3.2 Quantifying rarity

I defined rarity based on the local abundances of species. A commonly used definition of local rarity is the number of singletons, i.e. the number of species represented by a single individual within an assemblage (Maurer and McGill, 2011). Singletons are detected in many assemblages, especially in species-rich tropical ones, even with high sampling effort (Longino *et al*., 2002; Novotny and Basset, 2000). A less conservative, but strongly linked, definition of rarity is the number of singletons plus the number of doubletons, i.e. the number of species represented by two individuals. The advantage of using the expanded definition of singletons plus doubletons rather than only singletons is an increase in data and a decrease in statistical noise. For my analysis, I tested how both the number of singletons and the number of singletons plus doubletons are changing so I can be sure any effect detected is not sensitive to the definition used. I also analysed rarity change in terms of numbers of singletons, and in terms of Fisher's Alpha, which is a measurement of assemblage structure sensitive to rarity (Maurer and McGill, 2011). Although Fisher's alpha is a parameter of the logseries species abundance distribution model, this parameter is also useful for assessing assemblages that are not well fitted by the logseries model because it usually approximately equal to the number of singletons (Magurran, 2004, p 103).

The presence, and relative frequency, of singletons and doubletons is a commonly used measure of sample completeness (Chao, 1984; Colwell and Coddington, 1994; Mao and Colwell, 2005). However, to be included in the BioTIME database, sampling method must be kept consistent, and all data was rarefied before analysis to account for sampling effort. Changes in numbers of rare species are therefore unlikely to be artefacts of shifting sample completeness.

5.3.3 General trends in numbers of rare species

I assessed whether there is a systematic change in rarity, measured in terms of the number of singletons and doubletons, using a negative binomial mixed effect model using the R package *GLMMadaptive* (Rizopoulos, 2018). In this model, the number of singletons and doubletons each year was regressed against mean-centred year (**Equation 9a**). Assemblage ID was included as a random effect with varying slope and intercept to calculate individual assemblage rates of change, and a single overall slope was calculated for global rarity change. In addition, I calculated separate linear models

for each assemblage regressed against mean-centred year to estimate the number of significant slopes in either direction (**Equation 10**).

Equation 9. The negative binomial mixed model used to calculate rates of change of rarity. Model fit plots in (a) **Appendix Figure 18** and (b) **Appendix Figure 19**.

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i$$

$\mu_i = e^{\eta_i}$

$y_i \sim NB(\mu_i, \theta)$

η_i is the linear predictor of the number of rare species for value $_i$, quantified in terms of either number of (a) singletons and doubletons or (b) the number of singletons only

μ_i is the predicted value of η_i after transformation using the inverse of the log link function

y_i is the predicted number of rare species for x_i after including the error distribution

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

Equation 10. The linear model used to calculate separate rates of change of rarity for each assemblage, so that the significance of each slope could be assessed. This model was consequently applied separately to each assemblage.

$$\eta_i = \alpha + \beta x_i + \epsilon_i$$

η_i is the number of rare species for value $_i$, quantified in terms of number of singletons and doubletons

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the slope for mean-centred year

ϵ_i is the residual error

I tested for a difference between realms (marine, terrestrial and freshwater) by including realm as a fixed effect with an interaction with mean-centred year in the singletons and doubletons mixed model, and checked the significance of this interaction (**Equation 11**). I also assessed the potential influence

of central latitude and spatial grain on the resulting rates of change of singletons and doubletons by visually assessing scatter plots.

Equation 11. The mixed model regressing rarity against mean-centred year which includes an interaction effect of mean centred year and realm to assess whether realm type is influencing rarity change. Model fit plots in **Appendix Figure 20**.

$$\eta_i = \alpha + \beta x_i + m_i l_i + d(x_i + l_i) + b_j + S_j x_i$$

$\mu_i = e^{\eta_i}$

$y_i \sim NB(\mu_i, \theta)$

η_i is the linear predictor of the number of rare species for value $_i$, quantified in terms of number of singletons and doubletons

μ_i is the predicted value of η_i after transformation using the inverse of the log link function

y_i is the predicted number of rare species for x_i after including the error distribution

x_i is the mean-centred year for value $_i$ from dataset n

α is the overall intercept

β is the overall slope for mean-centred year x

l_r is the realm type r for value i

m_r is the overall slope for change in realm type r for value i

$d(x_i + l_r)$ is the interaction between mean-centred year and realm type

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

To check that my results were not sensitive to the breadth of the definition of rarity used, I ran another negative binomial mixed model, this time with singletons only regressed against mean-centred year and Assemblage ID as a random effect (**Equation 9b**). I also assessed change in Fisher's Alpha, which was calculated using the *fisher.alpha* function of the R package *preseqR* (Deng *et al*., 2016, 2015). The Fisher's Alpha value was regressed against mean-centred year using a mixed effect model with Assemblage ID as a random effect (**Equation 12**). This model was constructed using the *lme* function

of the R package *nlme* (Pinheiro J *et al*., 2018), and included a power of variance covariate structure given by the fitted values of the fitted model.

Equation 12. The mixed model regressing Fisher's alpha against mean centred year. Model fit plots in **Appendix Figure 21**.

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

$\epsilon_i \sim \sigma^2(v) = |v|^{2\theta}$

η_i is the Fisher's alpha value for value i,

x_i is the mean-centred year for value i from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

v is a variance covariate given by the fitted values η_i and θ is the variance function coefficient

ϵ_i is the residual variance

5.3.3 Rarity and immigration

To explore how rarity changes with species richness, I fitted a mixed model of $\log_2$ species richness change with the same structure as the rarity model except for a Gaussian error distribution (**Equation 13**). The strength and direction of the relationship between rates of change of rarity and rates of change of species richness for each study was compared with Pearson's Correlation coefficient using the *cor.test* R function.

Equation 13. The mixed model regressing species richness against mean-centred year. Model fit plots in **Appendix Figure 22**.

$$\eta_i = \alpha + \beta x_i + b_j + S_j x_i + \epsilon_i$$

η_i is the $\log_2$ species richness for value i,

x_i is the mean-centred year for value i from dataset n

α is the overall intercept

β is the overall slope for mean-centred year

b_j is the change in intercept for values with the random effect j

S_j is the change in slope for values with the random effect j

ϵ_i is the residual error

To directly test whether there are more rare species immigrating than going locally extinct within assemblages, I used a methodology developed by Dornelas *et al*. (2019). This analysis counts numbers of immigration and extinction events, and accounts for detection error by testing for random vs non-

random patterns of 0 abundances. To undertake this analysis, I first selected only rare species from the assemblages used in the above analyses. My selection criteria for rare species was any species that had a minimum population abundance of 1 or 2 within the assemblage. These criteria selected 14635 species populations. Some species were rare in more than one assemblage, and so accounted for multiple populations within the overall analysis. For each species population, the population abundances were converted to a string of binary presence and absence data (0s and 1s). I then counted the number of immigrations (transition between 0 and 1) and extinctions (transition between 1 and 0). To avoid detection errors inflating immigration and extinction events, I applied the *runs.test* function from the *tseries* R package (Trapletti and Hornik, 2018). This function tests whether the strings of 0s and 1s are random or non-random. Although there is some uncertainty in this method, I then treated significantly non-random strings of 0s and 1s as "true" immigration and extinction events. Species populations that only immigrated once into an assemblage were assigned to category "Immigration", and species that went extinct only once were categorised as "Extinct". Species that underwent more than one immigration or extinction event were categorised as "Multiple" Any species with population abundances of 0 and species without significant extinctions or colonisations were categorised as "Persistent".

5.4 Results

5.4.1 General trends in numbers of rare species

All of the assemblages used in this analysis - that is the assemblages with abundance quantified as counts of individuals - contained either singletons or singletons and doubletons.

I detected a significant increase in the number of rare species overall, defined in terms of singletons and doubletons (slope: 0.007, SE: 0.003, p: 0.038; **Figure 46A**). This systematic increase in rarity was supported by the results of the individual linear models, where 17 studies displayed significant increases in rarity and only 3 displayed significant decreases in rarity (**Figure 46B**).

There was no significant interaction between realm and time, suggesting that there are no notable differences between different realms (**Figure 47**). There was also no relationship between slopes of change of rarity and spatial extent (**Figure 48A**). There was no signal for a difference in slopes of change of rarity at different latitudes, but there are insufficient tropical data to comment on differences between tropical and temperate assemblages (**Figure 48B**).

The increase in rarity is less pronounced but still positive for rarity measured using numbers of singletons only (slope: 0.05, SE: 0.03, p: < 0.001, **Figure 49A**), and more pronounced in rarity measured using Fisher's Alpha (0.05, SE: 0.01, p: <0.001, **Figure 49B**). Changes in singletons correlate very closely

to changes in singletons and doubletons (Pearson's Correlation: 0.90, p: < 0.001). Changes in Fisher's Alpha also correlates positively but much less strongly with slopes of change of singletons and doubletons (Pearson's Correlation: 0.20, p: 0.05).

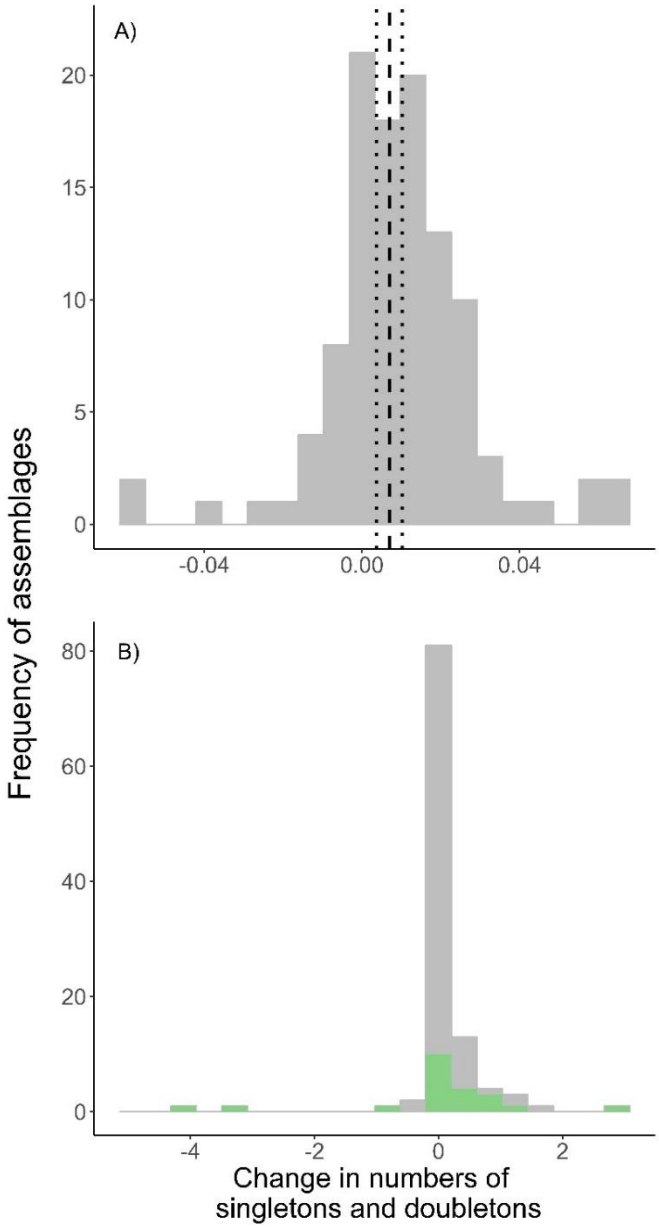


Figure 46. In panel (A) is the distribution of slopes of change in the number of rare species within assemblages (defined as singletons and doubletons) calculated from the mixed model. The vertical dashed red line represents the overall global trend in changing numbers of rare species, and the dotted black lines represent the standard error around this estimate. In panel (B) is the distribution of slopes of change calculated individually for each assemblage. The grey histogram shows all slopes, and the overlaid green histogram shows only significant slopes

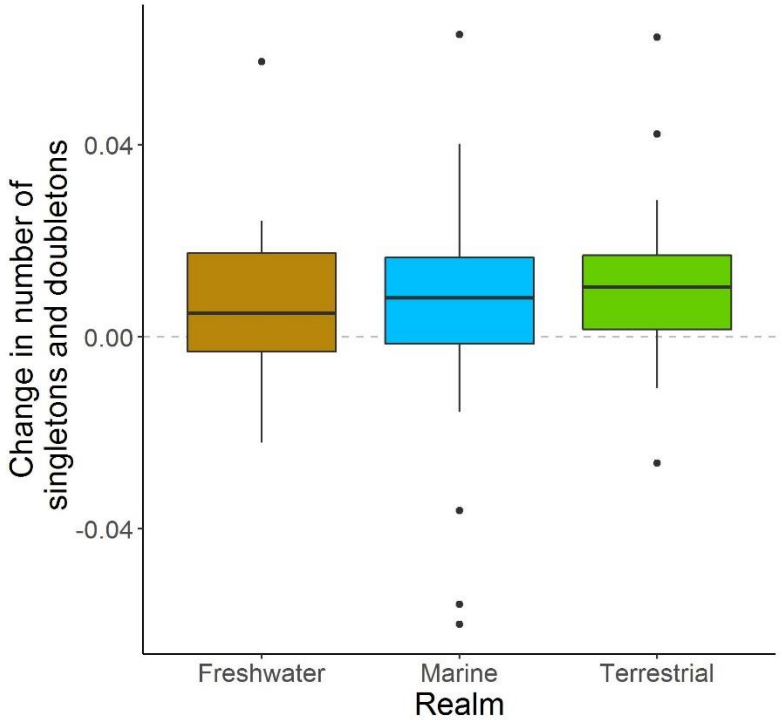


Figure 47. The rates of change of rarity calculated from the singletons and doubletons mixed model, split by realm. There is no clear difference between marine, terrestrial and freshwater systems.

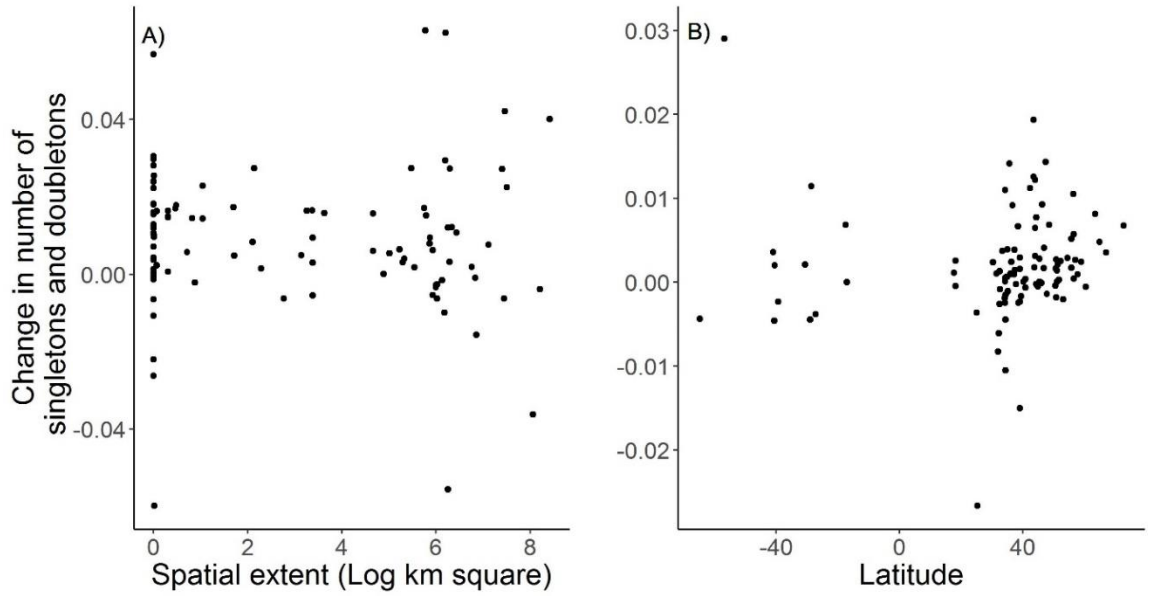


Figure 48. The rate of change of rarity calculated from the singletons and doubletons mixed model, plotted against (A) $\log_2$ spatial extent of each assemblage and (B) central latitude of each assemblage. There is no signal for a scaling effect or a difference across latitudes. .

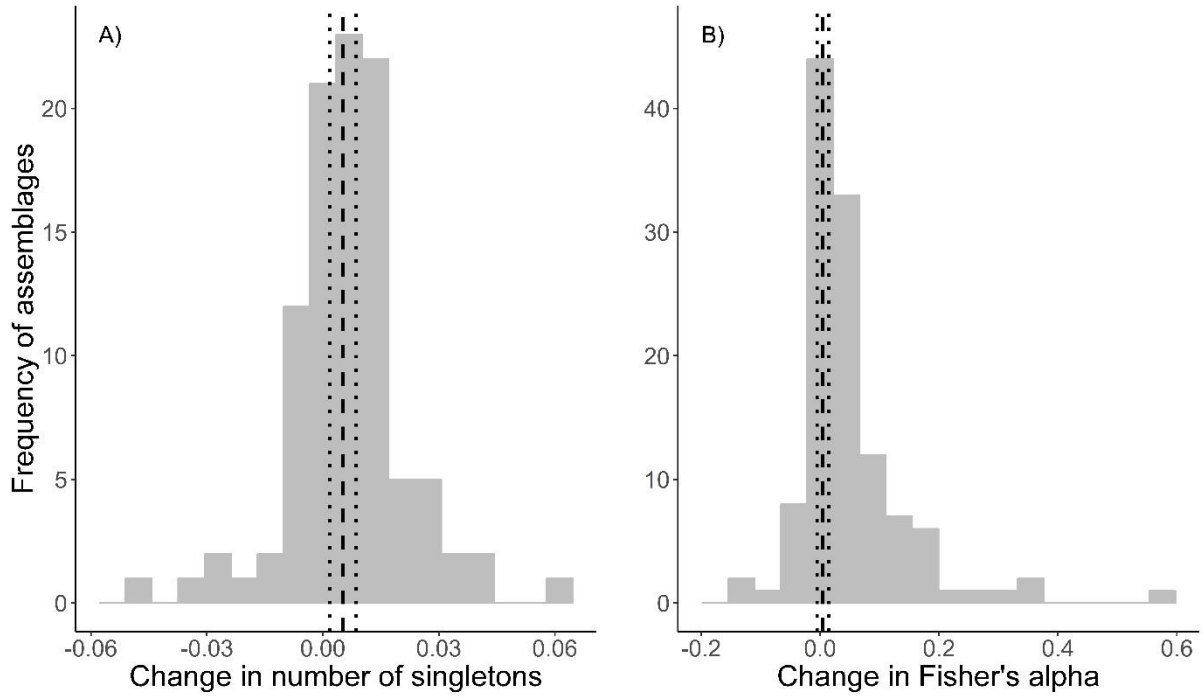


Figure 49. The distribution of slopes of change of the (A) number of singletons within assemblages and (B) Fisher's Alpha. The vertical dashed line represents the general trends calculated from the mixed models and the dotted black lines represent the standard error around these estimates.

5.4.3 Rarity and immigration

I detected a positive trend in species richness globally (slope: 0.0018, SE: 0.0009, p: 0.04; **Figure 50**). There is a positive relationship between a change in the number of rare species and a change in species richness within assemblages (Pearson's Correlation: 0.47; p: <0.001, **Figure 51**). This relationship was also seen when measuring rarity as the number of singletons (Pearson's Correlation: 0.47, p:<0.001, **Figure 52A**) and more weakly with Fisher's Alpha (Pearson's Correlation: 0.19, p: 0.05, **Figure 52B**).

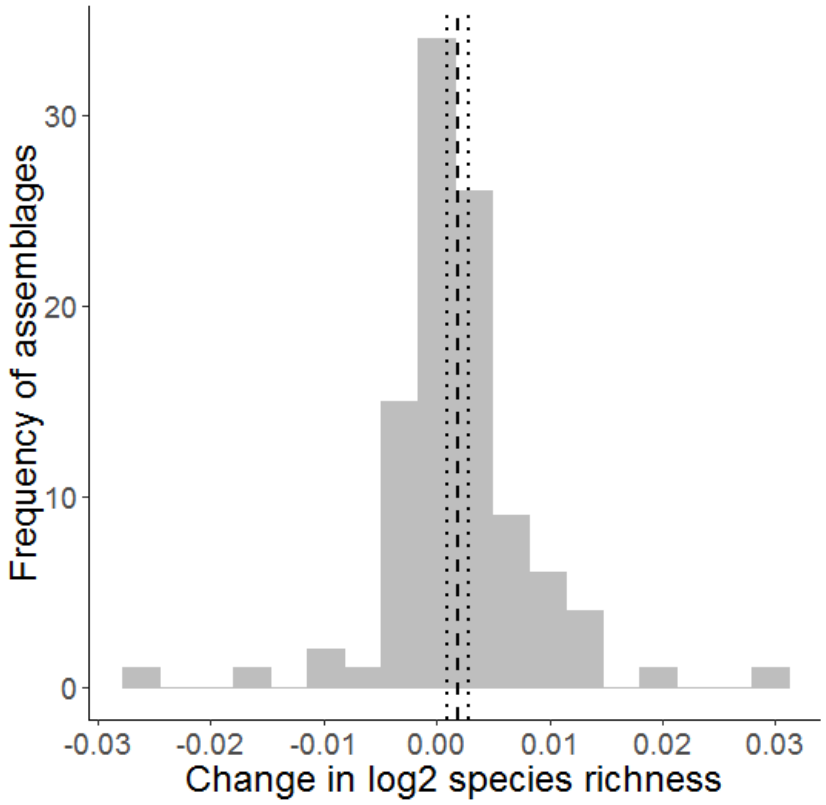


Figure 50. The distribution of slopes of change in assemblage species richness. The vertical dashed line represents the overall global trend in the number of singletons, as calculated from the mixed model. The dotted lines represent the standard error around this estimate.

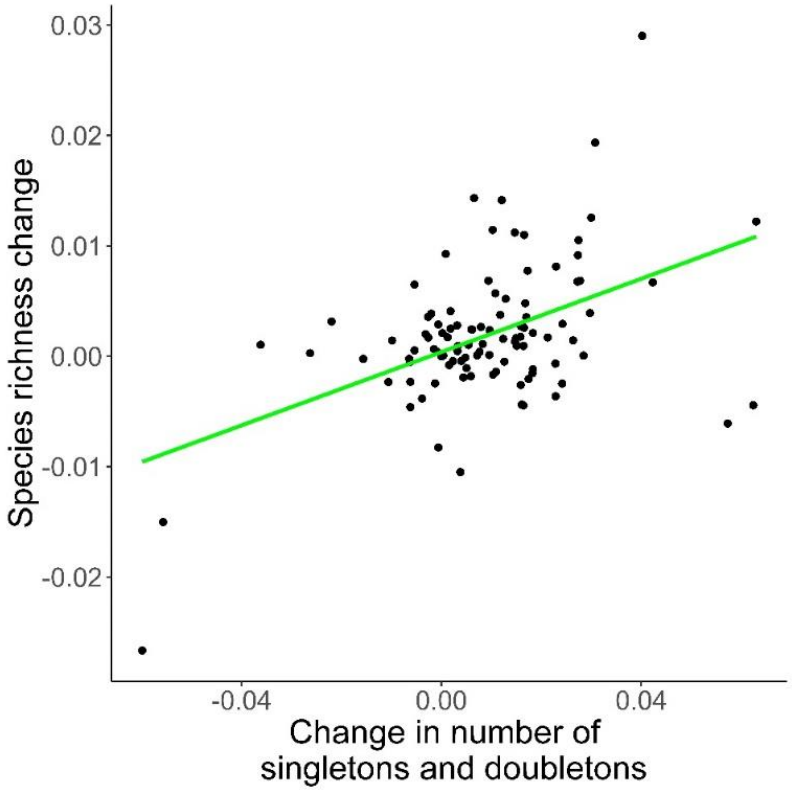


Figure 51. The relationship between the slope of change in the number of rare species (singletons and doubletons) and the slope of change in species richness within assemblages. The positive relationship is represented by a green line showing a linear trend.

Of the 14635 rare species populations tested, 12215 (83%) were persistent within assemblages. Of the rare species that were not persistent over time, 1618 (11%) underwent multiple immigration and extinction events, 518 (3.5%) immigrated into assemblages, and 284 (1.9%) went locally extinct (**Figure 53**).

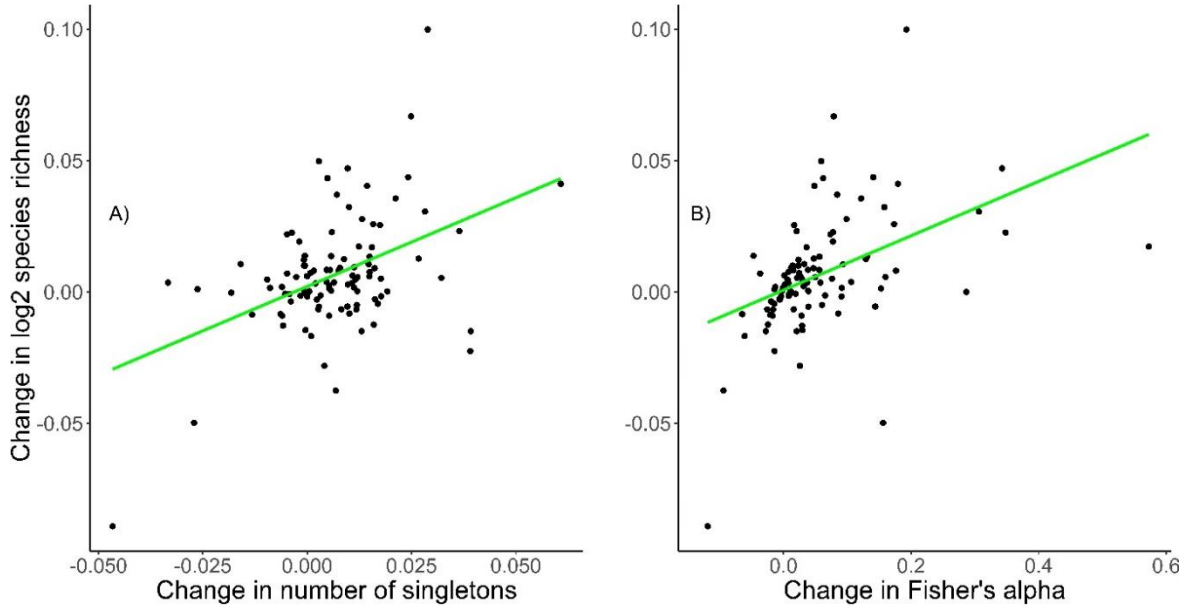


Figure 52. Rates of change of the (A) number of singletons and (B) Fisher's Alpha plotted against rates of change of species richness within assemblages. The positive relationships between assemblage metrics are represented by a green line showing the linear relationships.

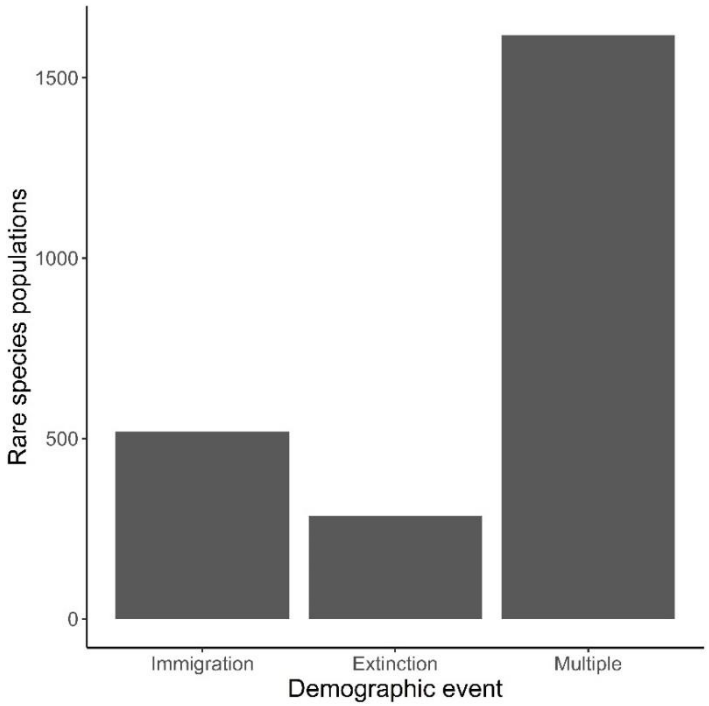


Figure 53. The number of rare species (defined as species with minimum population abundance of one or two within an assemblage) that immigrate (Immigration), go extinct (Extinction), or undergo multiple extinction and colonisation events (Multiple) throughout the time series.

5.5 Discussion

In line with my expectations, I found an increase in the number of rare species, defined as the number of singletons and doubletons, within assemblages (**Figure 46**). This result did not change when rarity was defined as the number of singletons (**Figure 49A**) or evaluated using Fisher's Alpha (**Figure 49B**). However, the overall increase in the number of rare species within assemblages was correlated with corresponding increasing species richness (**Figure 51**). This result, coupled with the higher number of rare species immigrating than going locally extinct, suggests that new species entering assemblages in low numbers are maintaining or increasing local species richness (**Figure 53**). This scenario suggests changes in the structure and identity of species present within assemblages in response to recent environmental change.

Detecting changes in the structure and identity of species present within assemblages is challenging, because focusing on individual facets of biodiversity, for example species richness or numbers of rare species, does not necessarily distinguish between modified and unmodified assemblages. For example, despite obvious threats to biodiversity globally, recent meta-analysis of species richness change found no evidence of systematic decline (Dornelas et al., 2014; Vellend et al., 2017, 2013). It was only by combining trends in species richness and rarity that I could start to understand the structural shifts within assemblages. To monitor and understand ecosystem change, we need to focus more on combining different facets of biodiversity.

Another issue in assessing biodiversity change within assemblages is that we never have complete samples, and so estimations of the completeness of sampling must take place. The ratio of singletons and doubletons within samples is often used to estimate sample completeness (Chao, 1984; Colwell and Coddington, 1994; Mao and Colwell, 2005). However, my results provide evidence of shifting numbers of singletons and doubletons even when sampling effort has been controlled for. This result suggests that the presence of rare species reflects more than just sampling incompleteness. Caution is needed when applying these sample completeness methods to detect changes in alpha diversity over time, even if sampling methodology remains consistent, because potentially important shifts in rare species numbers may be interpreted as changes in sample completeness instead.

That I found more immigration events amongst rare species than extinction events supports my suggestion that the increase in rarity I detected is likely strongly influenced by increasing numbers of species immigrating in low numbers. A recent assessment of immigration and local extinctions events across assemblages, however, found a balance of immigrations to extinctions (Dornelas et al., 2019). The inconstancy between my results of more immigrations of rare species vs Dornelas et al.,

(2019)'s result of balanced immigrations and extinctions suggests that the increase in immigration has not yet substantially permeated into the higher abundance classes of assemblages. The potential influence of these immigrant rare species will depend largely on whether this discrepancy is due to insufficient time passing for many of the newly arrived species to increase in abundance, or whether I am detecting an increase in transient species (Magurran and Henderson, 2003) that will not lead to increasing numbers of abundant immigrants but instead to a "transient biodiversity surplus" (Jackson and Sax, 2010).

It is clear from my results that there is substantial change within assemblages, which raises important questions around the causes and consequences of these shifts. Specifically, why are there more species immigrations? Human-mediated immigrants, often termed "invasive species", are one possible source of rare species. The success of some species in spreading across the world through human vectors is such that we should now perhaps consider increasing local species richness as the null expectation (Buckley and Catford, 2016). Because of the limited number of species that can utilise human activity to spread, increasing immigration of this sort may be contributing to biotic homogenization where only a few species win at the cost of many losers (Pereira et al., 2012). This is a concerning prospect because non-native species introduced by people tend to have specific functional traits that may differ a lot from native species, therefore an assemblage maintaining no net loss within assemblages because of extensive non-native introductions may still exhibit shifting ecosystem functioning (Buckley and Catford, 2016). It is therefore important for future work to assess the potential direction and magnitude of functional shifts as a result of increasing immigration.

Another possible driver of increased immigration could be climate change, as changes in the suitability of habitat can force species to colonise new regions (Jackson and Sax, 2010). For example, many species are shifting poleward as a response to increase temperatures (Hickling et al. 2006). The majority of the data used in my analysis is from temperate northern assemblages where climate migration is expected to increase colonisations. The relationship between species richness and rare species might be different in tropical assemblages where species are already close to biological limits. Further analysis of such systems is badly needed, but there is currently a dearth of good temporal assemblage datasets in these areas. The effects of increasing climate driven immigration is also on ecosystem functioning is also difficult to predict because vectors of movement are far more varied than for human-mediated immigrations (Buckley and Catford, 2016).

To conclude, I found evidence that the number of rare species locally is generally increasing, in part because more rare species are immigrating into assemblages than going locally extinct. My results

provide evidence of measurable changes in the structure of assemblages in the recent past, and raise questions about the potential impact of these immigrating species.

Chapter 6

General Discussion

The main aim of this thesis was to contribute to our knowledge and understanding of how assemblages change. My research has focused on assessing how different aspects of assemblage composition and structure have changed, with the goal of making informed suggestions on how to monitor biodiversity change effectively. In *Chapter 1*, I posed four related questions:

1. How influential is the sampling approach when estimating assemblage species richness and composition?
2. How closely do change in the currencies of abundance and biomass relate: do changes in one currency predict changes in the other currency?
3. Is there evidence for directional changes across assemblages?
4. What implications do my results have for understanding how biodiversity is changing at the local level?

In this final chapter I will provide an overview of my results to these questions, discuss how the answers increase our general understanding of biodiversity change, and suggest future research priorities.

6.1 How influential is the sampling approach when estimating assemblage species richness and composition?

There are substantial gaps in our understanding of biodiversity change, particularly at regional scales and tropical areas, so making the best use of existing data is a priority. An issue with existing data, however, is that sampling methodologies vary substantially between datasets. In *Chapter 2,* I showed that two very different data collection methods, a targeted survey and a historical museum collection, can provide surprisingly comparable estimates of species richness and the composition of species identities of freshwater fish in the rivers of Trinidad and Tobago. The systematic, targeted survey data is relatively typical of the types of data used in monitoring biodiversity; for example this is the type of data the BioTIME database generally comprises of. The historical museum collection data, on the other hand, is a data type that is fraught with potential issues because of its unsystematic collection methodologies and the potential difficulties of temporal scale. Despite these issues, the museum data suggested almost the same species richness value as the survey data (50 and 46 species, respectively) for the Trinidad and Tobago freshwater fish assemblages. My results therefore suggest a potential avenue for increasing the opportunity for monitoring regional scale turnover: using historical data as a baseline of species identities to compare with more recent survey data collection endeavours. It is worth noting, though, that issues of spatial scaling mean this result does not necessarily hold true for smaller or much larger scales.

Although the identities of species recorded within the two datasets were not the same, both datasets contained records for the common species. The two datasets differed in recording the presence of locally uncommon and narrowly distributed species. The presence of these locally rare species is considered ubiquitous within ecological assemblages (McGill *et al*., 2007), a statement that is supported by the fact that singletons and doubletons are present in all the BioTIME assemblages where abundance was quantified in terms of count data (*Chapter 5*). Thus, my results suggest that caution should be used if species-richness-only turnover metrics are used, for example the Jaccard index. This is because both datasets missed some of the rare species that are presumed to be present, and they did not miss the same species. The presence of very rare species may consequently vary substantially, and this variation is likely to inflate estimates of turnover. Since both datasets detected most species, excluding some of the very rare species, estimates of turnover focusing on these more abundant species are less likely to be affected by sampling error. If the more abundant core species are focused upon, therefore, then my results suggest that estimates of turnover in assemblage composition in terms of species identities present are likely to be robust between the two data collection techniques.

6.2 How closely do change in the currencies of abundance and biomass relate: do changes in one currency predict changes in the other currency?

Numerical abundance and biomass are two metrics of measuring assemblage size, and they capture slightly different information. Numerical abundance is closely linked to community dynamics, and biomass to resource allocation (White *et al*., 2007). Gaining more insight into how these metrics change will provide further insight into how species population dynamics and resource allocation may change over time and interact. This information has implications for understanding how assemblage composition and functioning may adapt to the increasingly disturbed conditions caused by anthropogenic pressures, because general trends are likely to be driven by the widespread effects of human activity on ecosystems. My results from *Chapter 3* suggest that, at the level of assemblage size, the currencies of numerical abundance and biomass are closely linked. An increase or decrease in one of these currencies was generally mirrored by a change in the same direction by the corresponding currency, meaning change in one currency generally predicted change in the other currency.

This result was contrary to my expectation that smaller-bodied individuals were increasingly replacing larger ones, thereby maintaining numerical abundance while biomass declined. Instead, my results suggest a lack of a strong trade-off between body size and abundance, and that instead the overall

standing capacity of systems is variable. This result has implications for changes in ecosystem functioning, because it shows that standing capacity of assemblages, which is such a fundamental element of ecosystem functioning, can vary in terms of both numerical abundance and biomass. On a more practical note, my result also suggests that at the assemblage level, changes in one currency may be inferred from changes in another, because change in the currencies positively co-varied.

In *Chapter 3* I also assessed a case study quantifying predation pressure on guppies in Trinidad and Tobago using both numerical abundance and biomass currencies. This study highlighted the fact that, at lower levels than assemblage size, changes in one currency may not infer changes in another currency. Numerical abundance and biomass provided different answers to questions related to how different sites were ordered on a predation pressure gradient, and how sites varied over time. Care therefore needs to be taken to choose most appropriate currencies of abundance for the question at hand. Because predation pressure is an important mechanism affecting guppy population dynamics (O'Steen *et al*., 2002; Reznick and Endler, 1982) and fish assemblage structure (Jackson *et al*., 2011), these results also show how inferences about the relative strength of different ecological mechanisms can be influenced by the currency used to measure abundance.

6.3 Is there evidence for directional changes in biodiversity across assemblages?

Ecosystems are under increasing pressure from anthropogenic sources, but how assemblages are adapting and changing to these new conditions is unclear. Elucidating general trends in how assemblages are changing is important for predicting future conditions, implementing effective conservation strategies, and improving our understanding of assemblage dynamics. In *Chapters 3-5*, I explored how different aspects of assemblage structure and composition are changing in the BioTIME database (**Table 12**). As mentioned above, I found no trends in assemblage size quantified in terms of either numerical abundance or biomass (*Chapter 3*). Contrary to my expectation, I also found no general trend in how the absolute or relative abundance of dominant species is changing (*Chapter 4*). Even when the abundance of the dominant species did change, it generally changed in the same direction as assemblage size, demonstrating that regulation of the dominance structure is common. It is worth noting, however, that my results on the lack of comparability between numerical abundance and biomass measurements in predator ensembles (*Chapter 3*) suggest caution in extrapolating numerical abundance results to biomass as well; there could be shifts in terms of the biomass of dominant species. I also found in *Chapter 4* that although the dominance structure is un-trending across assemblages, there is a suggestion that of increasing turnover in the identity of the dominant species.

That the above analyses found no general trends in assemblage size or dominance does not mean there are no general trends in other aspects of assemblages. I found evidence in *Chapter 5* of an increasing number of locally rare species across many assemblages, although there were some deviations from this general trend. This increase in rarity was linked more closely to increased immigration than to decreasing populations, a result that is supported by the increasing levels of turnover detected by Dornelas *et al*. (2014). A result that contradicts the results of Dornelas *et al*. (2014), however, is the increase in species richness detected in *Chapter 5*. Although my analysis used the same database at the Dornelas *et al*., (2014), I used a different subset that included only studies with at least 10 years of data and additional studies that were not available to the earlier by Dornelas *et al*. 's (2014) analysis. This increase in data may account for the inconsistency between my results of increasing species richness and Dornelas *et al.* 's result of no systematic change in species richness.

In conclusion, although the assemblage size and the abundance of dominant species are not changing systematically, there are increasing numbers of rare species entering assemblages, and these species may be driving increasing local species richness (**Figure 54**).

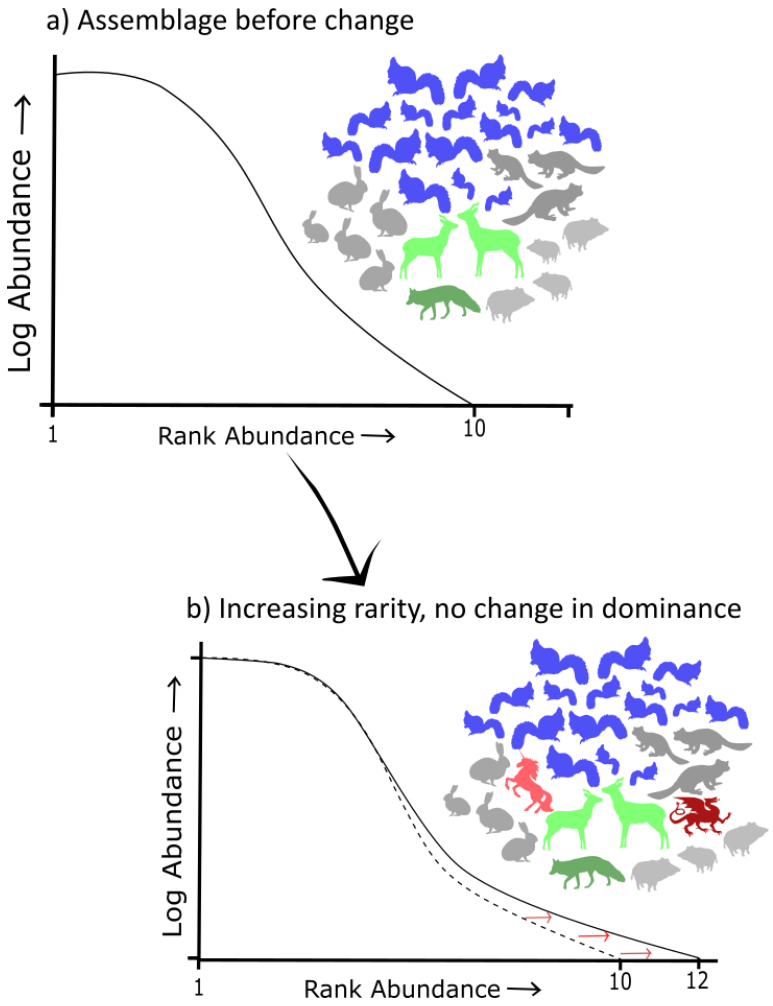


Figure 54. A schematic diagram of how assemblages are changing, according to the results of my thesis *Chapters 3-5*. In general, the assemblage size and the abundance of the dominant species remain relatively stable, whereas the number of rare species increases.

Table 12. The expected and observed trends in how different aspects of assemblage structure and composition are changing, according to my thesis analyses of the BioTIME database.

	Currency	Chapter	Expected trend	Observed trend
Assemblage size	Numerical abundance	3	No change	No change
	Biomass	3	Decrease	No change
Dominance	Absolute	4	Increase	No change
	Relative	4	Increase	No change
Body size	Average length or weight of dominant	4	Decrease	No change
Turnover	Turnover of dominant identity	4	Increase	Increase
Rarity	Number of singletons and doubletons	5	Decrease	Increase
Species Richness	Number of species	5	No change	Increase

6.4 What implications do my results have for understanding how biodiversity is changing?

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently published the summary for policymakers of their global assessment report on biodiversity and ecosystem services (Diaz *et al*., 2019). The main result of this extensive report was a dire warning about "nature's dangerous decline", because most indicators of ecosystem health are showing rapid decreases. Such a systematic and influential decline globally is at first glance in opposition to the general lack of general trends detected in my analyses. For example, the IPBES report states that native species populations have declined on average by at least 20%. Such a substantial decline is at odds with my results of no systematic decline in assemblage size (*Chapter 3*). A potential explanation for the discrepancy may lie in the fact that the BioTIME assemblages I analysed do not relate to habitats that have been substantially modified. The IPBES report suggests that 75% of the land's surface has been significantly altered, and 66% of the ocean area is heavily impacted by anthropogenic activities. Assemblage size in terms of both numerical abundance and biomass is variable, even amongst the relatively stable assemblages I focused on. The situation in the more heavily-altered assemblages may therefore be quite different from the general trends I found in my thesis. However, none of the assemblages included in the BioTIME database are pristine, because some drivers such as climate change and ocean acidification are wide-reaching. The choice of assemblages included in my

analyses are therefore unlikely to entirely explain the difference between my results and the IPBES results.

An alternative explanation is that there is a bias in which species populations are monitored. For example, the WWF living planet report (WWF, 2018) found a decline of 60% in wildlife populations. Such a high figure is at odds with both my results and the results of the IPBES report. However, the WWF report relies heavily on data on singe species instead of assemblages of species, and there is a bias for monitoring the populations of declining species. In my analysis, I did not differentiate between native and non-native species, and I included data from all species populations within the assemblage dataset. Understanding the dynamics of how assemblages change, which species are undergoing increasing populations even as other species decline, and the consequences of change for ecosystem functioning will help contextualise the results of large-scale reports such as the IPBES and the WWF reports.

In this section of my discussion, I will consider my results in terms of their implication for assemblage structural change. After this, I will discuss my results in relation to coexistence theory and ecosystem regulation, and then summarise how my thesis relates to best practice in measuring biodiversity change.

6.4.1 Increasing rarity

The results from my thesis demonstrate that assemblages are changing, but this process is complicated, variable and difficult to detect. Although I found evidence of increasing rarity, the mechanism behind this general trend does not follow many of my theoretical predictions. For example, a popular theory is that the survival probability of a species is directly related to its population size (Rohr *et al*., 2016). In this case, locally rare species are on the brink of extinction, whereas species with large populations are unlikely to go extinct. This assumption has empirical support, as the numerical abundance of a species was the strongest predictor of species persistence in studies by Suding *et al*., (2005) and Winfree *et al*., (2014). A potential mechanism for this population size-survival relationship is based on community assembly processes, where species richness and evenness decline under stressful situations due to species sensitivity to abiotic factors (Passy *et al*., 2017). Increasing environmental stress filters communities based on tolerance, where more tolerant species become more abundant and less tolerant species become less abundant, with rare species eventually being eliminated. Empirical evidence for this theory has been found in fish and diatom assemblages, particularly in high stress assemblages (Passy *et al*., 2017).

My results regarding increasing rarity, conversely, demonstrate that often there is no relationship between an increasing number of rare species and decreasing species richness. This suggest that in

many cases increasing rarity is not caused by populations declining and then eventually going locally extinct. My result is therefore in line with a recent analysis that found species with small populations were not more likely to go extinct than common species (Daskalova *et al*., 2018). These results highlight the fact that species may be rare for reasons other than declining habitat suitability. For example, the extent to which different species inhibit their own growth may also contribute to uneven assemblage abundances. Rare species could inhibit their own growth more than common species, and so live in lower densities (Comita *et al*., 2010). Soil pathogens, for instance, explain abundance differences in plant communities (e.g. Janzen, 1970; Klironomos, 2002; Mangan *et al*., 2010). Strong self-limiting tendencies may also be linked to strong positive growth rates at very low abundances, thereby allowing rare species to persisting at low densities (Yenni *et al*., 2012).

An alternative, or perhaps co-occurring, explanation for the increasing rarity detected by my analysis, which is supported by corresponding increases in species richness found in *Chapter 5*, is that there are more species immigrating into assemblages in low numbers. These rare species are therefore rare not because of their inherent population dynamics, but because they have not yet had the opportunity to become established. The increased immigration may be a consequence of the growing connectivity provided by human endeavours (Buckley and Catford, 2016), or increasing numbers of species migrating as a response to climate change (Hickling *et al*. 2006). Most likely, it is a combination of both sources of immigration, and in fact these two sources may act synergistically by facilitating pathways of migration for species seeking more appropriate climates. Teasing these two sources of immigration apart may prove informative, because the causes of immigration have implications for the prevalence of biotic homogenisation. The majority of species are unlikely to be able to take advantage of human pathways of migration, so the few non-native species introduced by anthropogenic activities are likely to exhibit a limited number of functional properties and potentially differ substantially from native species (Buckley and Catford, 2016; Van Kleunen *et al*., 2010). Immigration of “invasive” non-native species into habitats can bolster local species richness while decreasing spatial beta diversity (Kortz and Magurran, 2019). If immigrating species are consequently a relatively un-diverse group, then increased immigration may exacerbate issues of biotic homogenisation.

Other important questions raised by my results on increased rarity and immigration are: what proportion of these immigrating species will establish in their new assemblages, and what effect will they have on ecosystem functioning? Although I found no general trend in assemblage size across assemblages, there was great variation between individual assemblages (*Chapter 3*). This result highlights how variable fundamentally important elements of ecosystem functioning can be; changes in species identities and population sizes can affect functioning. The increase in immigrants I detected may largely be a consequence of an increase in transient species (Magurran and Henderson, 2003)

that do not contribute to ecosystem services. Such a situation is problematic, because when species richness is used as the metric of assessing change then swelling numbers of transients has the potential to hide very serious declines in functionally important core species.

6.4.2 Community structure

Because numerically dominant species often strongly influence the functioning of assemblage (Massaccesi *et al*., 2015), shifts in the dominance structure may have serious consequences for ecosystems. When disturbed, one prediction is that assemblages will become increasingly dominated by one or a few very common species. This is because abundant generalist species will often increase in population size while less adaptable specialist and rare species will decline in population size (Dornelas, 2010; Simons *et al*., 2015). A classic example of this is seen in assemblages undergoing pollution disturbance (Gray and Mirza, 1979; Kim *et al*., 2013; Ugland *et al*., 2007). That the dominance structures, at least in terms of the population size of the most numerically abundant species, did not generally increase in my datasets (*Chapter 4*) was surprising considering how modified most assemblages globally are considered to be. Even though assemblages included in the BioTIME database do not include extremely modified, transformed habitats like grasslands converted from forests, the influence of humans on ecosystems is sufficiently pervasive that there are very few if any truly undisturbed assemblages. That immigration is generally increasing across assemblages (*Chapter 5*) is a tangible example of change, as is the increase in turnover detected by Dornelas *et al*. (2014) and the suggestion of increasing turnover of dominant species identity found in *Chapter 4*. It is also worth noting that dominance did increase in many assemblages I analysed, but these cases were balanced by decreases in dominance within other assemblages.

It is clear that how assemblages are adapting to change is more varied and complex than the theory of disturbance and competitive advantage describes. For example, assemblages with very similar dominance structures can still have quite different compositions in terms of the species present and how abundant each individual species is (Komonen and Elo, 2017). This is important because changes in the identity of dominant species can substantially influence ecosystem functioning, irrespective of changes in the dominance structure (Wohlgemuth *et al*., 2016). I detected increased turnover of dominant species identities in *Chapter 4* as well as increased immigration in *Chapter 5*, which suggests that the rise in turnover detected by Dornelas *et al*. (2014) likely permeates throughout the entire dominance structure instead of being only a function of increasing transient species. Predicting the effects of shifts in the dominance structure and species identities will prove challenging because, although dominance and functional diversity are linked, the relationship is complicated. A decrease in dominance could increase or decrease the effectiveness of an ecological function, depending on how

effective at that specific function the most dominant species is (Wohlgemuth *et al*., 2016). Even though dominance may be stable, then, the ecosystem functioning may be changing.

6.4.3 Implications for coexistence theory

Most models and theories exploring assemblage structure and composition assume a limited resource and consequently a stable assemblage size, although this property is often phrased in terms of "zero-sum dynamics" or "community capacity" (Ernest *et al*., 2008). This assemblage property is, in fact, fundamental to the influential Theory of Neutral Ecology (Hubbell, 2001). However, my results from *Chapter 3* show that assemblage size in terms of both numerical abundance and biomass is variable, which suggests the amount of resources available for niche partitioning is also variable. Linking shifts in assemblage size directly to disturbances and drivers of change was outwith the scope of this thesis, but my results do raise some interesting questions regarding disturbance and assemblage structure. For example, does disturbance increase or decrease niche space and resource availability for species? On one hand, a disturbance might cause the loss of some resources and niches. One the other hand, new conditions may lead to new niches, thereby potentially increasing resource availability for the whole assemblage. Disturbance has been theoretically predicted to increase diversity through the Intermediate Disturbance Hypothesis by impeding highly effective competitors from overly dominating assemblages, but only when the disturbance reduces all species densities evenly (Connell, 1978). Although the Intermediate Disturbance Hypothesis has recently come under some criticism on empirical and theoretical grounds (Fox, 2013), there is still substantial evidence (Kershaw and Mallik, 2013) and theoretical support (Sheil and Burslem, 2013) for this hypothesis. This situation is unlikely in many cases, however, because generalist species are often favoured over specialist species under increasing anthropogenic pressure (Clavel *et al*., 2011). Generalists increasingly dominating assemblages could decrease assemblage size because there is a trade-off between a species efficiency and effectiveness at accessing a resource vs the breadth of resources it can access (Futuyma and Moreno, 1998).

That the dominance structure is generally retained even when assemblage size changes (*Chapter 4*) also suggests that there are mechanisms at work maintaining the relative niche space of species. Although the r-K species continuum provides a useful starting point for exploring these mechanisms, ecological systems are far more complicated than a single continuum can describe. To this end, contemporary coexistence theories distinguishes between stabilising niche differences and relative fitness differences (Chesson, 2000). Stabilising niche differences arise when negative frequency dependence occurs, that is when individuals of a species suppress their own population growth more than other species populations (HilleRisLambers *et al*., 2012). Such situations arrive, for example,

through resource partitioning or species attracting host-specific enemies. This mechanism of population density self-regulation serves to prevent competitive exclusion by superior competitors. Relative fitness differences, on the other hand, are the competitive differences between species in the absence of stabilising niche differences (HilleRisLambers *et al*., 2012). These relative fitness differences strongly influence the relative abundance of species within assemblages; superior competitors are expected to have larger populations than inferior competitors, as long as stabilizing niche differences are not too limiting.

Changes in the abiotic conditions such as the climate are likely across most of the assemblages I analysed, because anthropogenic disturbances and modifications are common globally. Increasing turnover (Dornelas *et al*., 2014) and immigration (*Chapter 5*) are changing as well because biotic conditions are reliant on specific species interactions and finesses. It is interesting, then, that even when conditions change so much that assemblage size increases or decreases, the dominance structure remains relatively stable (*Chapter 4*). This result suggests that changes in assemblage size are not been driven by increases or decreases in the abundance of dominant species, despite the possibility that generalist dominant species may increasingly dominate assemblages because they are better adapted to increasingly disturbed conditions. Instead, dominant species retain their relative abundance, which suggests they also maintain their proportion of niche space and resource availability. Dominant species must therefore also retain a fairly constant fitness relative to other species in the assemblage, because fitness differences are intricately linked to realised niche space. Alternatively, stabilising niche differences may be acting sufficiently strongly upon the dominant species that their own population density precludes increases in populations, thereby avoiding competitive exclusion of less fit species. Regardless, my results suggest that the number and size of realised niches of the species within the modified assemblage are not altered with changes in assemblage size.

6.4.4 Ecosystem resilience

That some aspects of assemblages, such as numbers of rare species and turnover, are showing systematic shifts, whereas other aspects such as species richness, assemblage size and the dominance structure are remaining relatively stable (**Table 12**). This suggests that ecosystems are resilient to some but not all types of change. The potential mechanisms behind this resilience are varied and hold important information for understanding ecosystem functioning and predicting change.

The increasing immigrations I detected in *Chapter 5* may hold the key to understanding one element of ecosystem resilience under increasing anthropogenic disturbance. For assemblages to remain stable, there must be the opportunity for compensatory extinctions and immigrations (Brown *et al*.,

2001). High dispersal promotes stability through compensatory dynamics (Steiner *et al*., 2011). Adaptive migrations, where species move to areas they are better adapted to, are predicted to support relatively stable biomass even when assemblage composition differs substantially (Allhoff *et al*., 2015). Even assemblages with very different structures can achieve similar sets of functions (Gallagher *et al*., 2013). The potential for species turnover to contribute to ecosystem stability is so great that Oliver *et al*., (2015) suggest it might be the very thing that allows resilient functions because species may be replaced by new, better adapted species with similar function.

Although increasing turnover may play an important part in sustaining many functions at the assemblage level, it may still have important implications for ecosystems and global biodiversity. Biotic homogenisation is likely to be occurring worldwide because there are only a few species that are well adapted to thriving in anthropogenically-influenced habitats, whereas there are many species that will decline or even go extinct. Certain traits may be favoured, for example smaller, more abundant species are expected to dominate under more disturbed conditions according to the r-K species continuum theory (Warwick, 1986). According to this theory, in a reasonably undisturbed habitat, numerical dominants are usually r-strategist species. These species are out of equilibrium with their resources, and show more stochasticity in their population dynamics. Biomass dominants, conversely, are usually a few large K-strategist species whose populations are closely aligned to their resources. Larger species are also more at risk because they often require larger fragmented or undisturbed areas, and they are also more vulnerable to overhunting. I found no evidence of declining body size in *Chapter 3*, nor declining body size of dominant species in *Chapter 4*, but I did not explicitly test body size distributions across assemblages. There are also many other functional properties of species that biotic homogenisation threatens, such as the ability to adapt to new conditions or to survive disease outbreaks. Weighing the positive and negative effects of increasing turnover within assemblages is consequently complex and requires a nuanced view of the ecosystem in question. It is clear, however, undertaking conservation management to promote ecosystem adaption is essential for sustainable and effective conservation endeavours (Webster *et al*., 2017).

6.4.5 Measuring biodiversity change

Heterogeneity in the ability of biodiversity measurements to detect change has received considerable attention in the literature. For example, Lamb *et al.* (2009) evaluated the statistical power of four approaches to analysing biodiversity: 1) traditional species richness and Simpson's diversity indexes, 2) species intactness indexes based on occurrence, 3) species intactness indexes based on abundance, and 4) multivariate community indexes that compare the community in question to a baseline expectation community. The authors also considered the ecological relevance and ease of

communication. They found that detectability of change differed between approaches, for instance they concluded that species richness was more powerful than the Shannon and Simpson's diversity indices in detecting change. However, when they assessed the identity of species, they found that the change detected was a positive change due to non-native species arriving. The Shannon and Simpson's indexes also lacked the ability to monitor species turnover, and are therefore unsuitable for quantifying temporal beta diversity. Lamb *et al.* (2009) suggested that relying on these biodiversity indexes to detect negative change is a mistake as any changes are likely to be detected too late. It is clear, therefore, that some consideration of statistical methods for evaluating datasets is necessary when calculating biodiversity change.

The variability in my results in terms of detecting change in assemblages highlights the dangers in relying on a single metric to monitor change. Even when I did find a signal for systematic change in the number of rare species (*Chapter 4*), it took a combination of two metrics (the number of rare species and species richness) to detect the underlying increasing immigration. There is consequently a need to use multiple aspects of biodiversity when monitoring change. Species richness is often used as a proxy for other aspects of assemblages (Isbell *et al*., 2017), but this metric alone is not effective by its self at detecting most signals of change.

The dominance structure of assemblages often reacts to change more quickly than species richness or assemblage size (Chapin *et al*., 2000). This reactivity, combined with the ecologically relevant information held in the relative abundance of species, means shifts in the dominance structure can elucidate how assemblages change over time (Matthews and Whittaker, 2015). However, my results from *Chapters 4* and *5* caution against assuming extrapolating from change in one section of assemblage structure to other sections. Although I found no evidence of a systematic shift in the very abundant dominant species of assemblages, I did find increasing numbers of rare species. This suggests that shifts in assemblage structure may be driven more by changes amongst the rare species than common species. Although it is logistically easier to focus on the abundance of only common species, such monitoring may miss key structural changes within assemblages.

One potential option is to focus on the intermediately abundant species, on the assumption that very abundant species can have too much variability, and there is too much uncertainty around presence of rare species (Gray and Mirza, 1979). Alternatively, species abundance distributions could be very useful for monitoring change, understanding biodiversity and supporting conservation (Matthews and Whittaker, 2015). Recent developments in quantifying species abundance distributions using the gambin model allow for the skewness of distributions to be calculated with a single alpha parameter (Matthews *et al*., 2014a). This model generally fits most assemblage structures well and provides a

useful opportunity for quantifying changes in assemblage structure. The alpha parameter measures the complexity of an assemblage's interactions with its environment (Ugland *et al*., 2007). Assemblages with complex interaction, and so a high "dimensionality", are closer to lognormal than logseries species abundance distributions. This property relates closely to our understanding of the effects of disturbance on assemblage structure, because increasing disturbance such as pollution is predicted to increasingly influence the structure of the assemblage, leading to a more uneven structure as the assemblage is "forced" by the disturbance (Ugland *et al*., 2007).

6.4.6 Baselines of change

The question of whether biodiversity is changing as a response to anthropological pressures requires an *a priori* expectation of what biodiversity would be doing otherwise. No biological system is completely static, so some background turnover of relative abundances and species identities is to be expected. Humans have also been modifying habitats for longer than we have been monitoring change, so whatever timeseries we assess will potentially have issues of shifting baselines, where we may not detect change because it has taken place before we started monitoring. In this case caution is needed when assessing change in decadal scale datasets because the study system might have already undergone severe changes before monitoring took place.

Some interesting questions raised by my analyses are: how static do we expect the community structure to be, and how much turnover should we consider normal? For example, what is our *a priori* expectation for how long dominant species remain dominant, or how much turnover there should be among rare species? In my analysis of the dominance structure in *Chapter 4*, I attempted to address this question with a cyclical null model which preserved within-species temporal autocorrelation, but broke species cross-correlations in abundance. This model involved 1000 iterations, where each iteration of the null model entailed randomly shifting the abundances of each species within each assemblage, and then applying the mixed model analysis. The cyclical null model removed interactions between species each year but maintained within species population dynamics. My logic behind this model was that random variation between species population dynamics was the expectation if the dominance structure is not changing as a response to a driver. This assumption, however, has some flaws in that regardless of external drivers, species interact with each other. For example, compensatory dynamics relies on species interactions. Theoretically, if increased disturbance and immigration weakens the ties between species in assemblages, then we might conversely predict an increased random relationship between population dynamics of different species. Such a situation calls for a very different structure of null model than my cyclical null model. Building appropriate

expectations to test empirically observed dynamics against requires a greater understanding of assemblage change and population dynamics.

Another issue for setting appropriate baselines is that ecologists rarely have complete data at the assemblage level. Even very intensely sampled systems still have lots of singletons and doubletons present, suggesting there are undetected species present (Longino *et al*., 2002). This issue of detectability becomes particularly troublesome at regional and larger scales. The Trinidad and Tobago freshwater fish assemblage I explored in *Chapter 3* is a prime example of the difficulty in gaining good baselines for regional comparisons, because regardless of the methodology used, species were missing from the sample. While rarefaction and extrapolation can account for this issue in terms of estimating changes in species richness, turnover analysis will always be influenced by incomplete species lists.

6.5.2 Non-linear change

My assessments of how assemblages change in *Chapters 3-5* have all focused on linear change. Most change in ecology is not linear though, and biodiversity change can potentially be better predicted by considering non-linear dynamics (Dippner and Kröncke, 2015). Such non-linear change in ecosystems is often called a regime shift, although the exact definition for what a regime shift is varies somewhat. In the narrower sense of the concept, a regime shift takes place when an assemblage switches between two or more stable states over a relatively short time span (Mantua, 2004). More broad definitions of regime shifts do not require switches between stable states, only abrupt and substantial changes (Collie *et al*., 2004). Regime shifts are difficult to predict, making long term predictions of biodiversity change difficult (Müller *et al*., 2014). Accounting for these non-linear changes when assessing assemblage dynamics may serve to elucidate assemblage structure and resilience mechanisms.

6.5.3 Issues of scale

The scale at which assemblage analysis takes place can strongly influence results. For example, while local scale species richness is not generally declining (Dornelas *et al*., 2014; Vellend *et al*., 2017, 2013), there is strong evidence for increasing extinctions (Diaz *et al*., 2019). Thus, global species richness is highly likely to be declining substantially even though local species richness is not. Understanding how biodiversity is changing therefore requires explicit consideration of the scales at which data are collected and analysed (Chase *et al*., 2019). Applying such a principle to a meta-analysis of very different taxa, like I have done in much of this thesis, provides challenges for the application of this principle. One option for overcoming scaling issues for analysing the BioTIME database is spatially gridding all datasets to a set grid size (i.e. Blowes *et al*., 2018). I chose not to pre-grid my data for my

analyses because 1. Spatial scale varies with a taxonomic entity's life history and size, so for example what is "local" to a whale is not necessarily "local" for a shrimp, and 2. Spatially gridding large datasets leads to increased issues of autocorrelation within analysis as one dataset can contribute to many similar trends. Instead, I chose to retain the spatial integrity of each dataset in the BioTIME database, thereby trusting that the data collectors made ecologically relevant decisions regarding the spatial extent of an assemblage for their study system. This does mean, though, that some of the assemblages in my dataset were arguably estimating gamma diversity rather than alpha diversity because their spatial extent was so large (i.e. the US Breeding Bird Survey spans the whole of the USA). Decisions on how best to account for scale need to be carefully decided upon on a case by case basis, and the implications of scaling considered.

6.6 Future research priorities

6.6.1 Species abundance distributions

My results from *Chapters 4* and *5* provide seemingly conflicting evidence about how the evenness of assemblages is changing, because the dominance part of the species abundance distribution seems stable even though the "tail" of rare species is generally growing. A more complete understanding of how the species abundance distribution in its entirety is changing is needed to fully understand how the structure of assemblages is changing. Closing this research gap is particularly pressing in light of the fact that evenness reacts faster than species richness to changes in the environment (Chapin *et al*., 2000), and these changes can have consequences for species interactions and ecosystem function (Hillebrand *et al*., 2008).

One potential avenue for assessing change in assemblage structure is to assess how the general shape of the species distribution changes over time using the Gambin model's alpha parameter that I described in Section 6.4.5 *Measuring biological change* (Ugland *et al*., 2007). Alternatively, functional regression, where a whole statistical function is regressed instead of a single parameter, provides an opportunity of detecting which part of the species distribution is changing (Matthews *et al*., 2017; Yen *et al*., 2015). As I demonstrated in my analysis of predator pressure quantification in *Chapter 3*, however, care needs to be taken when choosing appropriate currencies for defining the abundances of species, because relative species abundances quantified in terms of biomass may vary substantially from those quantified in terms of abundance (Henderson and Magurran, 2010). Ideally, analysis of species abundance distributions should consider multiple currencies within analyses for a more nuanced and informative answer (Morlon *et al*., 2009).

An alternative and potentially very informative rout regarding assessing assemblage structure is to focus on how different groups of species' abundance distributions change. For example, different guilds within assemblages can have different temporal dynamics (Magurran and Henderson, 2018), and functionally different groups of species, such as generalists and specialists, respond differently to change (Matthews *et al*., 2014b). Transient species can have also differently-shaped species abundance distributions to resident core species, where core species abundances tend to be lognormally distributed, and transients tend to have a log-skewed abundance distribution (Magurran and Henderson, 2003). Assessments of increasing multimodality of species abundance distributions could be used to test whether the different parts of assemblages are increasingly reacting differently to change. For example, we know there is multimodality present in BioTIME (Antão *et al*., 2017), but is there increasing multimodality over time? This question is pertinent because increased environmental heterogeneity such as anthropogenic disturbances can cause increasing multi-modality (Dornelas *et al*., 2009). Improvements to methods for testing shifts in the species abundance distribution are making questions regarding multimodality increasingly feasible, for example tests for multimodality in species abundance distributions have been incorporated into the Gambin species abundance distribution model (Matthews *et al*., 2019). Such analyses have the potential for elucidating assemblage stability mechanisms, particularly in relation to compensatory dynamics.

6.6.2 Functional traits and species turnover

An important question for future biodiversity is how pervasive the increase in turnover within assemblages (Dornelas *et al*., 2014) is, and how it is influencing ecosystem functioning. The results of *Chapters 4* and *5* of my thesis suggest that there is increasing turnover in both dominant and rare sections of the species abundance distribution, but as yet we do not know the potential impacts of this turnover. Quantifying this effect is particularly challenging because how important a species presence and abundance is to ecosystem functioning depends on the function you are assessing (Gamfeldt and Roger, 2017). In addition, shifts in the variety of functional traits can be substantially decoupled from shifts in species richness (Törnroos *et al*., 2019), so assessing changes in functional traits can be challenging.

Body size is a key functional trait to focus on when looking at ecosystem functioning (Norkko *et al*. 2013). When assessing shifts in body size of dominant species in *Chapter 4,* I focused on whether smaller species were increasingly becoming dominant. While I saw no evidence to support this hypothesis, I did see decreases in within species body size across dominant fish species. These results suggests that changes in body size may generally be more highly influenced by decreasing body size

within species. There are many reasons to expect body size to be generally decreasing within assemblages. For example, size spectra have been used in soil and marine communities to detect effects of human activities, where slope of the size spectra gets steeper in more heavily impacted assemblages, meaning there are fewer large individuals and more smaller ones (Petchey and Belgrano, 2010). Fish body size also decreased on a coral reefs due to human exploitation (Zgliczynski and Sandin, 2017), and shrinking body size is a response to climate change on palaeontological- and ecological timescales (Sheridan and Bickford, 2011). In terms of population dynamics, smaller species are also less likely to go extinct because they tend to have higher population densities (Cardillo, 2003).

A potential difficulty with undertaking meta-analysis of shifts in the body size distribution within assemblages is the lack of appropriate data. While databases such as the PanTHERIA and FishBase databases I utilised in *Chapter 4* provide the opportunity for linking species level traits to assemblage databases such as BioTIME, aggregating to species level can be problematic (Petchey and Belgrano, 2010) . I saw evidence of this in my analysis of changing dominant species body size, where aggregate fish species body size analyses suggested no directional change in body size whereas within-species body size analysis suggested general decreases in body size. Because of this, I believe that assessing shifts in the individual body size spectra of assemblages may be more useful in detecting body size changes than focusing on species-average body size distributions. This will be especially important for taxa continue growing after reaching sexual maturity, and so have the capacity for substantial shifts in body size distributions within generations.

The End.

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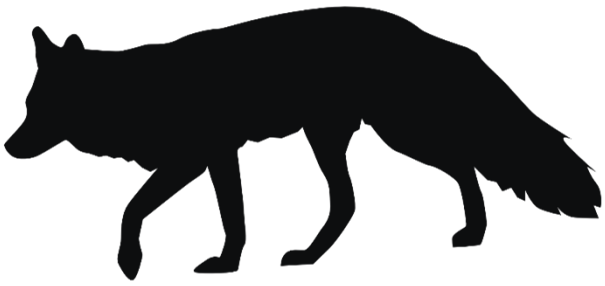

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Appendix

Appendix Chapter 2

Appendix Table 1. A breakdown of all freshwater fish potentially found in Trinidad and Tobago, along with extra information taken from the comprehensive list and key (Phillip *et al*., 2013) and Fishbase (www.fishbase.de/).

Distribution, habitat specificity and *status* descriptions can be found in **Table 1** of *Chapter 2*. *Diet* and *size* were taken directly from the comprehensive list and key. Fish found in the targeted survey are listed as "yes" in the *Survey* column, and those found in the museum collection data are listed as "yes" in the *Museum* column. *Red list status* was taken from fishbase.org. the "fishbase distribution" column information is taken directly from fishbase.org. If Trinidad and Tobago is explicitly mentioned in the fishbase distribution, then the species is listed as "yes" in the *fishbase found in trinidad and Tobago* column. If the distribution does not explicitly mention Trinidad and Tobago, but includes an area with Trinidad and Tobago in it, then the fish is listed as a "maybe" in this column. The *notes* column incudes any other potentially useful information.

Order	Species	Size (mm)	Distribution	Habitat specificity	Diet	Status	Survey	Museum	Red list status	FishBase distribution	FishBase found in Trinidad and Tobago
Achiridae	*Achirus novoae*	106	wide			native				South America: Orinoco basin, including delta.	
Anguillidae	*Anguilla rostrata*	1500	wide	specific	Carnivore	native	Present	Present	Endangered	Northwest to western Central Atlantic: Greenland south along the Atlantic coast of Canada and the USA to Panama, and throughout much of the West Indies south to Trinidad.	yes
Anostomidae	*Leporinus friderici*					transient				South America: Suriname and Amazon River basin (Ref. 36801). Reported from Argentina (Ref. 9086).	
	Aspredinichthys filamentosus	218		specific		native				South America: lower portions of coastal rivers and in	

										coastal waters in Venezuela to Brazil.	
	Aspredinichthys tibicen	240		generalist	Carnivore/omnivore	native				Central and South America: lower portions of coastal rivers and in coastal waters from Venezuela to northern Brazil.	
	Aspredo aspredo	410		generalist	Carnivore/omnivore	native				Central and South America: lower portions of coastal rivers from Venezuela to northern Brazil.	
	Platystacus cotylephorus	370		specific		native				Central and South America: Venezuela to northern Brazil (including the lower portions of coastal rivers).	
Auchenipteridae	*Pseudauchenipterus nodosus*	250	intermediate	generalist	Omnivore/ detritivore	native		Present		South America: Lower reaches of rivers and into estuaries from Venezuela to Brazil, at least to Bahia, including southern Trinidad.	yes
	Trachelyopterus galeatus	220	narrow	specific	Carnivore	native				South America: Widespread in northern South America.	
Callichthyidae	*Callichthys callichthys*	180	intermediate	generalist	Omnivore	native	Present	Present		South America: Colombia and Trinidad to La Plata River basin east of the Andes.	yes
	Corydoras aeneus	80	intermediate	generalist	Omnivore	native	Present	Present		South America: Colombia and	yes

										Trinidad to La Plata River basin east of the Andes.	
	Corydoras melanistius					transient				South America: Coastal rivers of the Guianas.	
	Hoplosternum littorale	230	intermediate	specific	Omnivore	native	Present	Present		South America: Most Cis-Andean South American river drainages north of Buenos Aires, Argentina (Ref. 37395). Introduced in the USA (Ref. 104645).	
	Megalechis picta					transient				South America: Amazon and Orinoco River basins, as well as coastal rivers of the Guianas and northern Brazil.	
Characidae	*Astyanax bimaculatus*	150	wide	generalist	Omnivore	native	Present	Present		South America: Panama to the Amazon basin.	
	Brycon amazonicus					transient			Least Concern	South America: Amazon River and its main tributaries in Brazil; Orinoco and Essequibo River basins.	
	Brycon falcatus	600	narrow	generalist	Omnivore					South America: Rivers in Guyana, Suriname and French Guiana; Amazon and Orinoco River basins.	
	Corynopoma riisei	80	intermediate	generalist	Carnivore	native	Present	Present		South America: coastal rivers of	yes

										Trinidad and northern Venezuela and from the Meta River basin.	
	Gephyrocharax valencia	60	narrow	specific	Omnivore	Recent Colonist	Present			South America: Valencia Lake tributaries and Guarico River basin in Venezuela.	
	Gymnocorymbus bondi	60	narrow	generalist	Omnivore	native				South America: Orinoco River basin.	
	Hemibrycon taeniurus	80	intermediate	specific	Omnivore	native	Present	Present		Central America: western Trinidad.	yes
	Hemigrammus ocellifer					transient				South America: Rivers of Guyana, Suriname, French Guiana, and Amazon basin in Brazil and Peru.	
	Hemigrammus unilineatus	40	wide	generalist	Omnivore	native	Present	Present		Central and South America: River basins of Trinidad, coastal river basins of Venezuela, rivers of Guyana, Suriname, French Guiana; Amazon and Guaporé River basins.	yes
	Hyphessobrycon axelrodi	30		generalist		native				Central America: Trinidad.	yes
	Odontostilbe pulchra	50	intermediate	generalist	Carnivore	native	Present	Present		Central America: Trinidad Island in Trinidad and Tobago; widespread in río Orinoco basin, smaller coastal drainages of Venezuela, Lake Valencia system	yes

										and the rio Essequibo basin. A spot occurrence in the upper rio Demini, rio Negro, Amazonas basin, though represented by a unique mature male.	
	Roeboides dientonito	120	wide	specific		Recent Colonist	Present	Present		South America: Lake Maracaibo and Orinoco River basin, and rivers of the northwestern portion of Guyana.	
	Triportheus auritus	260	narrow	generalist	Omnivore	Recent Colonist		Present		South America: Amazon River, Brazil.	
Cichlidae	*Andinoacara pulcher*	160	wide	generalist	Omnivore	native	Present	Present		Central and South America: Trinidad and Venezuela.	yes
	Cichlasoma taenia	220	wide	generalist	Carnivore	native	Present	Present		South America: Trinidad and northeastern Venezuela.	yes
	Cleithracara maronii					transient				South America: Trinidad (impersistent), Orinoco River basin (delta), rivers from Barima River (Guyana) to Ouanary River (French Guiana).	yes
	Crenicichla frenata	130	intermediate	specific	Carnivore	native	Present	Present		South America: Trinidad and northeastern Venezuela.	yes
	Crenicichla saxatilis	220	intermediate	generalist	Carnivore	native				South America: Atlantic coast	yes

										drainages of Suriname, French Guiana, Guyana, Venezuela and Trinidad.	
	Oreochromis mossambicus	600	wide	generalist	Omnivore	introduced	Present	Present	Near Threatened	Africa	
	Oreochromis niloticus	600	wide	generalist	Omnivore	introduced				Africa	
Curimatidae	*Steindachnerina argentea*	110	narrow	generalist		native	Present	Present		South America: Orinoco River basin, Caribbean versant rivers of Venezuela and Trinidad.	yes
Eleotridae	*Dormitator maculatus*	600	intermediate	generalist	Omnivore	native	Present	Present	Least Concern	North to South America: along the Atlantic slope from North Carolina (USA) to southeastern Brazil.	
	Eleotris amblyopsis	100	intermediate	intermediate-specific	Omnivore	native			Least Concern	North to South America: Atlantic drainage between South Carolina, USA and to French Guiana.	
	Eleotris pisonis	150	wide	generalist	Omnivore	native	Present	Present	Least Concern	Northwest to western Central Atlantic: Bermuda, Bahamas, South Carolina and northern Gulf of Mexico in USA to southeastern Brazil.	
	Gobiomorus dormitor	600	intermediate	generalist	Carnivore	native	Present	Present	Least Concern	Western Central Atlantic: Southern Florida and southern Texas in USA to eastern Brazil. Eastern	

										Central Atlantic: Macias Nguema (Fernando Po).	
	Guavina guavina					transient			Least Concern	Western Atlantic: southeastern USA to Brazil.	
Erythrinidae	*Erythrinus erythrinus*	200	narrow	specific	Carnivore	native	Present			Central and South America: Amazon and Orinoco River basins and coastal rivers of the Guianas.	
	Hoplias malabaricus	560	intermediate	generalist	Carnivore	native	Present	Present		Central and South America: Costa Rica to Argentina in most rivers basins.	
Gasteropelecidae	*Gasteropelecus sternicla*	65	intermediate	specific	Insectivore	Recent Colonist	Present	Present		South America: Peruvian Amazon, intermediate Amazon, the Guianas and Venezuela (Ref. 39056). Recorded from the Paraguay basin (Ref. 81048).	
Gobiesocidae	*Gobiesox nudus*	170	intermediate	specific	Insectivore	native	Present	Present	Least Concern	Western Atlantic: Bahama Is., Greater Antilles, Virgin Is., Lesser Antilles, northern South America	yes
Gobiidae	*Awaous banana*	300	intermediate	specific	Carnivore/omnivore	native	Present	Present		North, Central and South America: northern Florida, USA southward through the Greater and Lesser Antilles to Trinidad and Tobago, and from Tamaulipas, Mexico	yes

										southward to Caracas, Venezuela; central Baja California Sur and Sonora, Mexico southward to Tumbes, Peru.	
	Ctenogobius fasciatus	75		specific	Carnivore/omnivore	native			Least Concern	Western Central Atlantic: Mexico (Ref. 26938), Costa Rica to Venezuela, Dominica, Trinidad and Barbados.	yes
	Ctenogobius pseudofasciatus	70		specific	Carnivore/omnivore	native			Least Concern	Western Atlantic: east coast of Florida, USA.	
	Evorthodus lyricus	150	intermediate	specific	Carnivore/Omnivore	native		Present	Least Concern	Western Atlantic: Chesapeake Bay, USA and northern Gulf of Mexico to northern South America; absent in the Bahamas, but present in Greater Antilles.	
	Lophogobius cyprinoides	100		specific	Omnivore	native			Least Concern	Western Atlantic: Bermuda, Florida (USA), and the Bahamas to Central and northern South America	maybe
	Sicydium plumieri	140	intermediate	specific	Herbivore	native		Present	Data deficient	Central America: Caribbean Islands in Antilles south of Cuba.	yes
	Sicydium punctatum	100	wide	specific	Herbivore	native	Present	Present	Least Concern	Western Central Atlantic: Caribbean coast of Venezuela, Dominica, Jamaica, Martinique, Puerto	yes

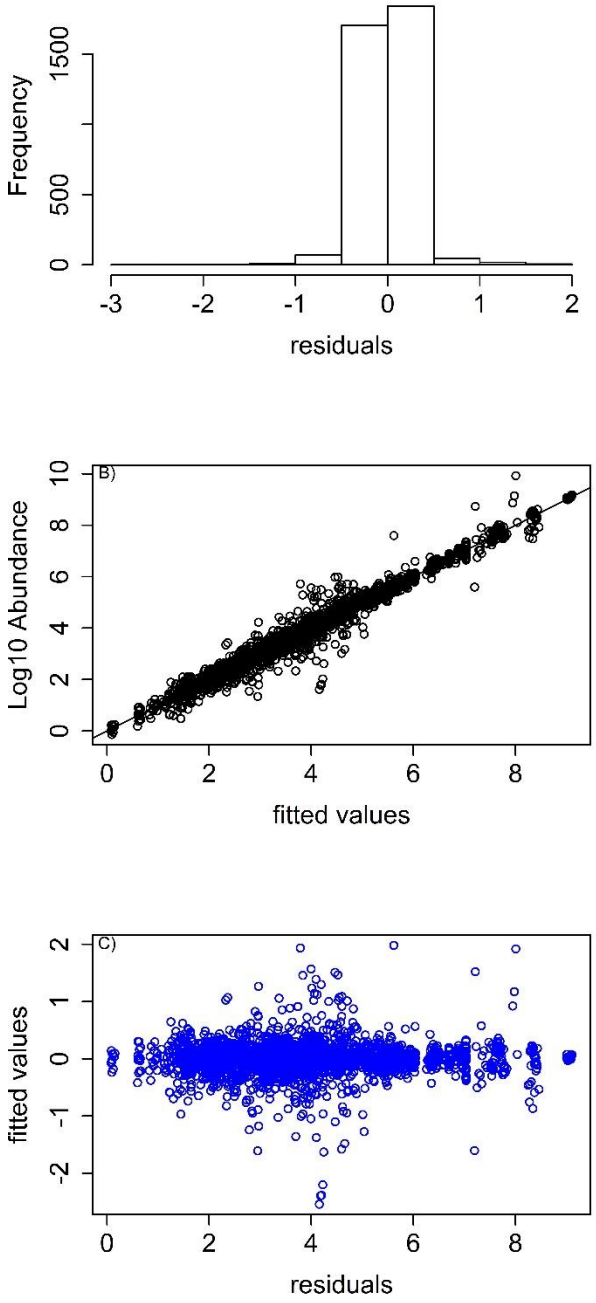
										Rico, Trinidad & Tobago (Ref. 50190) and Panama (Ref. 51464).	
Gymnotidae	*Gymnotus carapo*	760	intermediate	specific	Carnivore	native	Present	Present		Central and South America: southern Mexico to Paraguay, including Trinidad.	yes
Heptapteridae	*Rhamdia cf. quelen*	480	intermediate	generalist	Omnivore	native	Present	Present		Central and South America: Mexico to central Argentina.	
Hoplerythrinus unitaeniatus	*Hoplerythrinus unitaeniatus*	250	narrow	generalist		native	Present			Central and South America: São Francisco, Amazon, Paraná, Orinoco and Magdalena River basins, and coastal rivers in Guyana, Suriname and French Guiana.	
Lebiasinidae	*Copella arnoldi*	50	intermediate	specific	Carnivore	introduced	Present	Present		South America: lower Amazon, coastal Guianas to mouth of the Orinoco River.	
	Nannostomus unifasciatus					transient				South America: Parts of the Amazon basin of Bolivia, Brazil, and probably Colombia; the upper Orinoco basin of Venezuela, and Guyana.	
	Pyrrhulina laeta	90	narrow	generalist	Carnivore	introduced				South America: presumed to be central and upper Amazon River Basin.	
Loricariidae	*Ancistrus maracasae*	100	intermediate	generalist	Herbivore/detritivore	native	Present	Present		Central America: Maracas River basin	yes

										in Trinidad and Tobago.	
	Hypostomus robinii	200	intermediate	generalist		native	Present	Present		Central America: Trinidad.	yes
Mugiliidae	*Agonostomus monticola*	360	intermediate	specific	Omnivore	native	Present	Present	Least Concern	North to South America: North Carolina, Florida, Louisiana and Texas in the USA to Colombia and Venezuela, including the West Indies.	yes
Osphronemidae	*Trichopodus trichopterus*	200	narrow	specific	Carnivore	introduced			Least Concern	Asia: Mekong basin in Laos, Yunnan, Thailand, Cambodia and Viet Nam; Southeast Asia (Ref. 27732). Introduced elsewhere (Ref. 2847).	
Poeciliidae	*Poecilia boesemani*	40	narrow	generalist	Omnivore	native	Present	Present		Central America: Trinidad and Tobago.	yes
	Poecilia picta	50	wide	generalist	Omnivore	native		Present		Central and South America: Trinidad to the Amazon River delta.	yes
	Poecilia reticulata	65	wide	generalist	Omnivore	native	Present	Present		South America: Venezuela, Barbados, Trinidad, northern Brazil and the Guyanas.	yes
	Poecilia vivipara	50	wide	generalist	Omnivore	native	Present			America: between Suriname and Brazil (not the Atlantic area South of the Laguna dos Patos basin in Brazil);	maybe

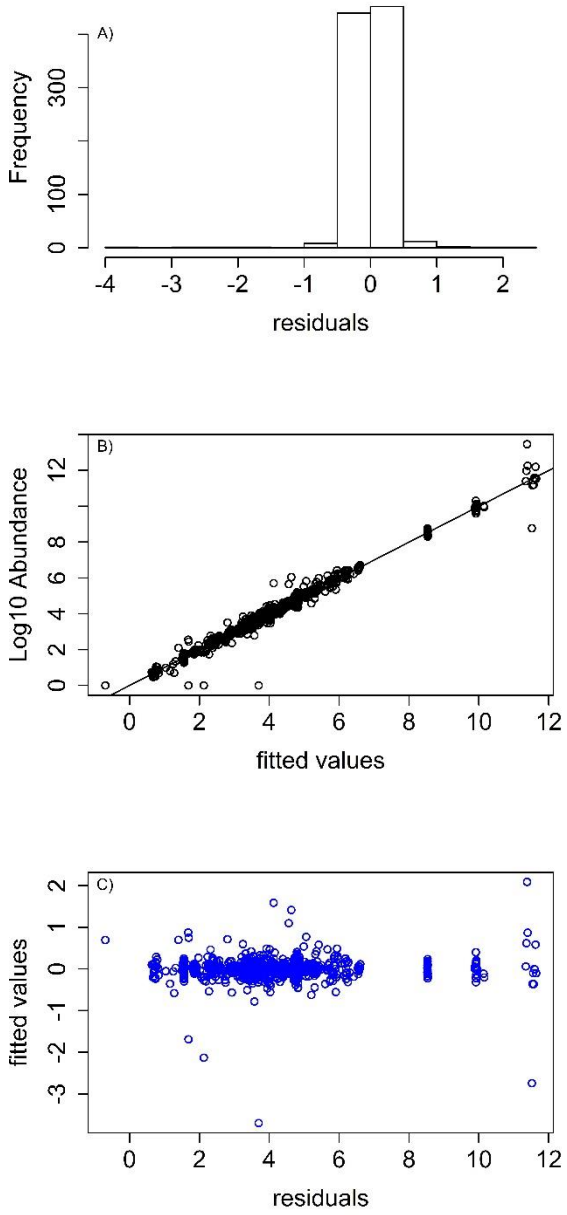
										introduced to the Caribbean.	
Polycentridae	*Polycentrus schomburgkii*	100	narrow	generalist	Carnivore	native	Present	Present		South America: Trinidad (W.I.), and Atlantic coastal rivers of Venezuela, Guyana, Suriname, French Guiana and Brazil (state of Amapá).	yes
Rivulidae	*Anablepsoides hartii*	110	wide	generalist	Carnivore	native	Present	Present		South America: Caribbean coastal river basins.	maybe
	Kryptolebias marmoratus	80	narrow	generalist	Carnivore/omnivore	native			Least Concern	North, Central and South America: eastern coasts of Florida (Indian River to Key West) in USA and Bahamas to Cuba, Jamaica, Cayman Island, Brazil, French Guiana, the Netherlands Antilles, Venezuela, Belize, Mexico, Puerto Rico. Throughout Caribbean (Ref. 26938).	maybe
Sygnathidae	*Pseudophallus mindii*	160		generalist					Data deficient	Central and South America: Atlantic and Caribbean coastal rivers.	maybe
Synbranchidae	*Ophisternon aenigmaticum*	800	wide	generalist	Carnivore	native				Central America: throughout the Atlantic Slope of Guatemala and Mexico to Cuba.	maybe

	Synbranchus marmoratus	1500	wide	generalist	Carnivore	native	Present	Present		Central and South America: Mexico to northern Argentina.	maybe

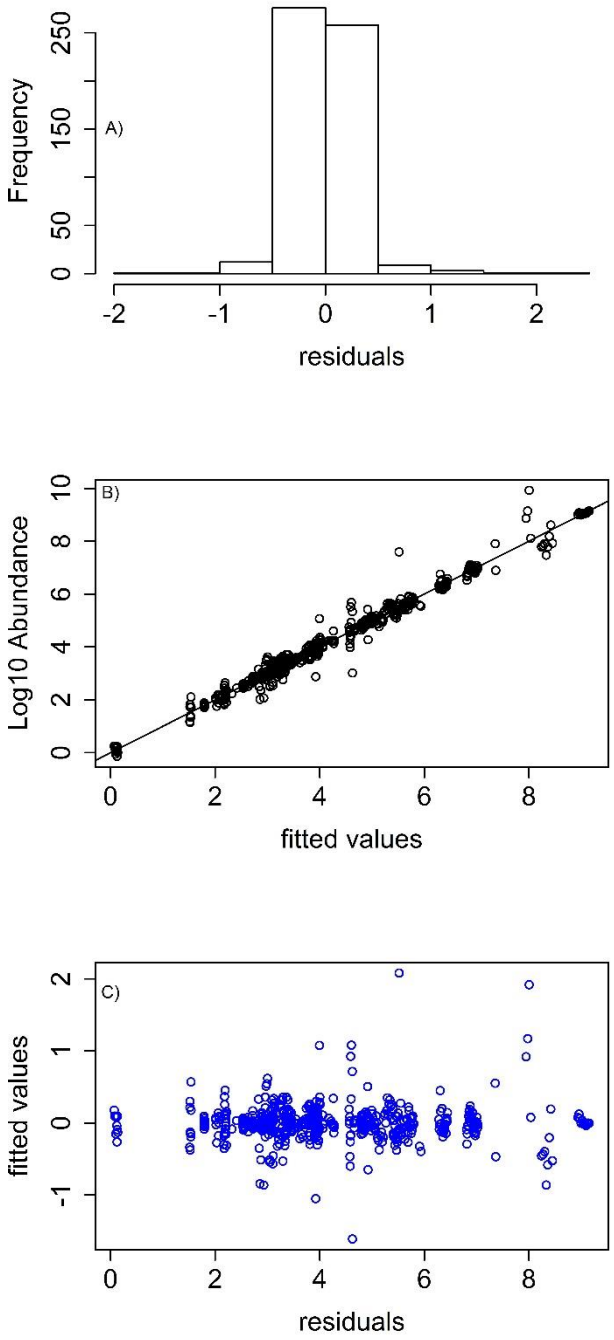
Appendix Chapter 3



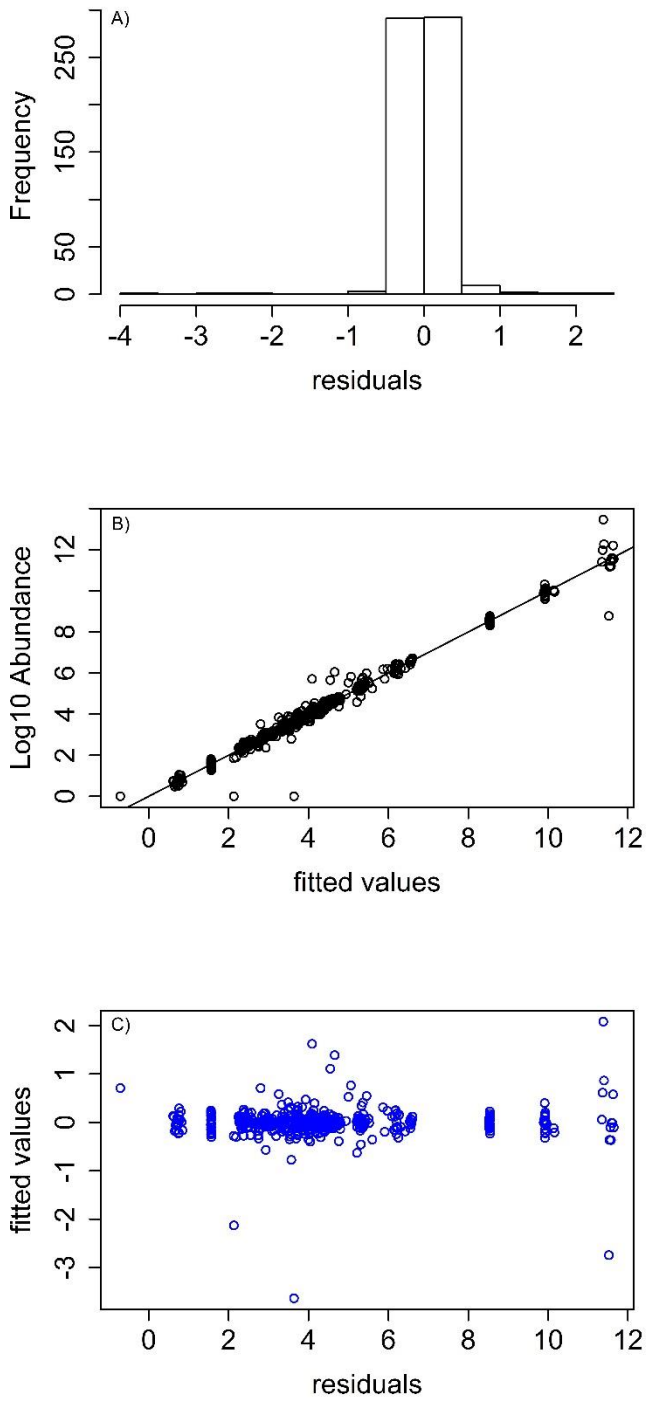
Appendix Figure 1. The model fit of the mixed effect model Equation 1a, regressing the $\log_2$ abundance within each assemblage against mean centred year. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).



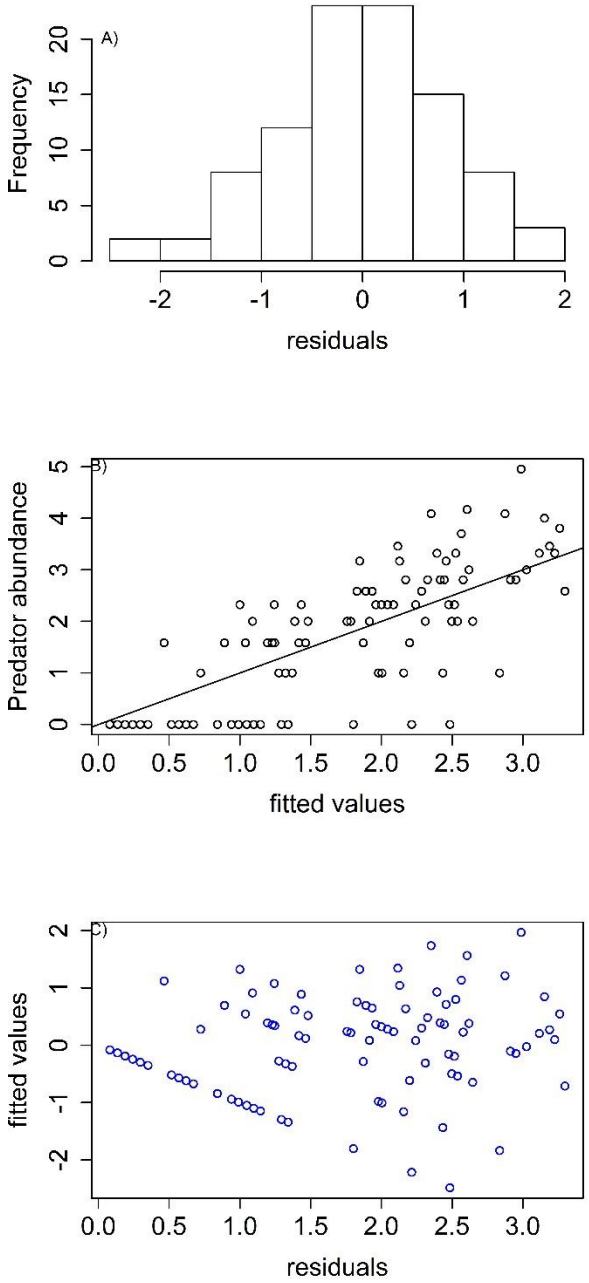
Appendix Figure 2. The model fit of the mixed effect model Equation 1b, regressing the $\log_2 + 1$ biomass within each assemblage against mean centred year. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).



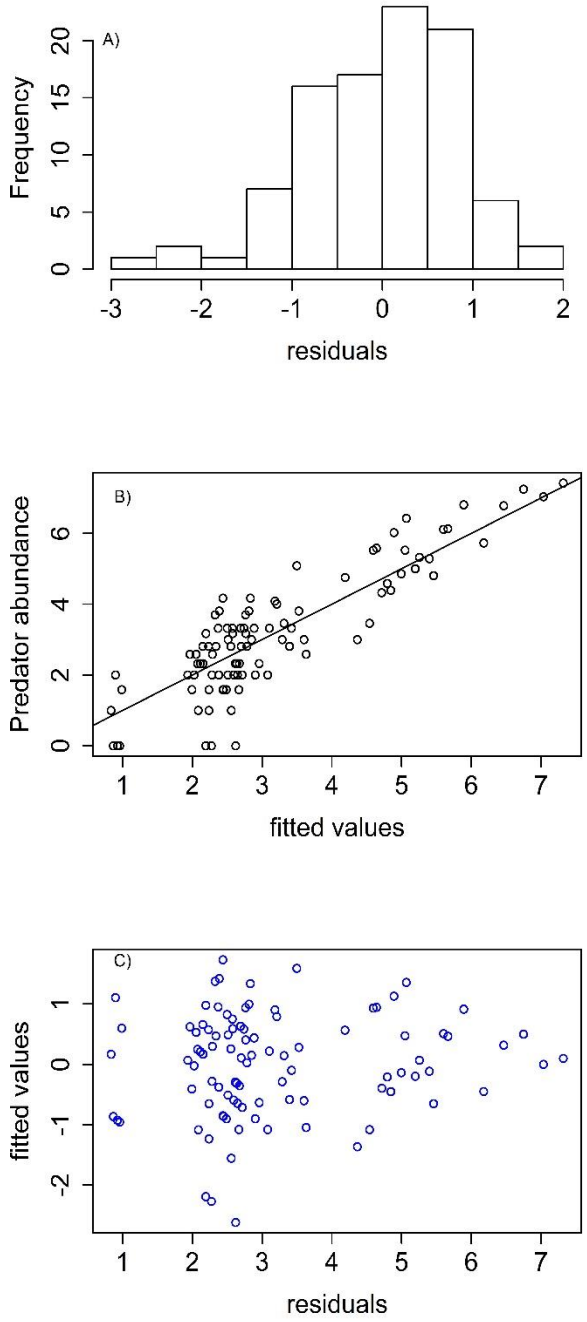
Appendix Figure 3. The model fit of the mixed effect model Equation 2a.3, regressing the $\log_2$ abundance within each assemblage against mean-centred year, with taxonomic group included as a fixed effect with no interaction effect. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).



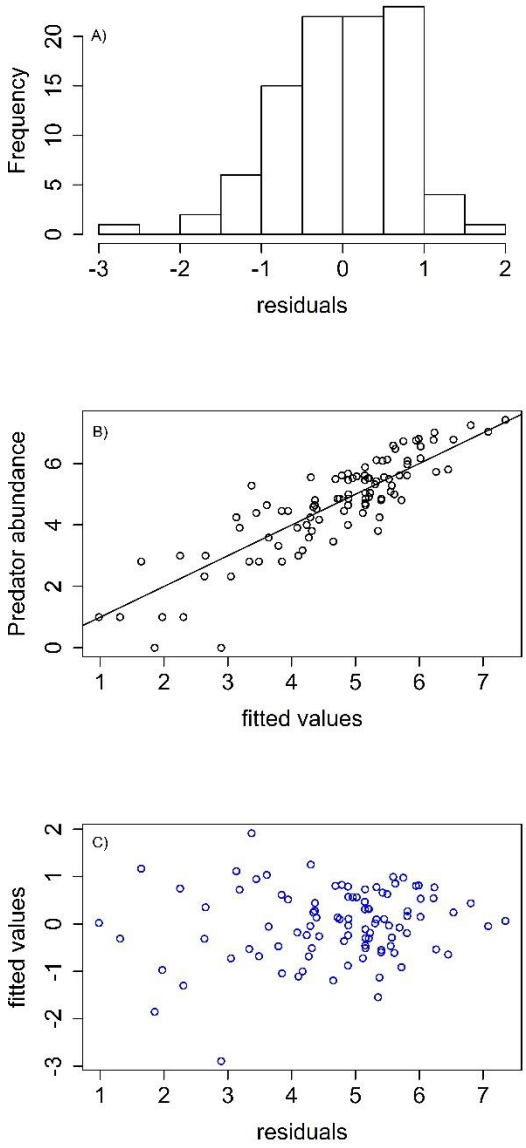
Appendix Figure 4. The model fit of the mixed effect model Equation 2b.3, regressing the $\log_2 + 1$ biomass within each assemblage against mean-centred year, with taxonomic group included as a fixed effect with no interaction effect. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).



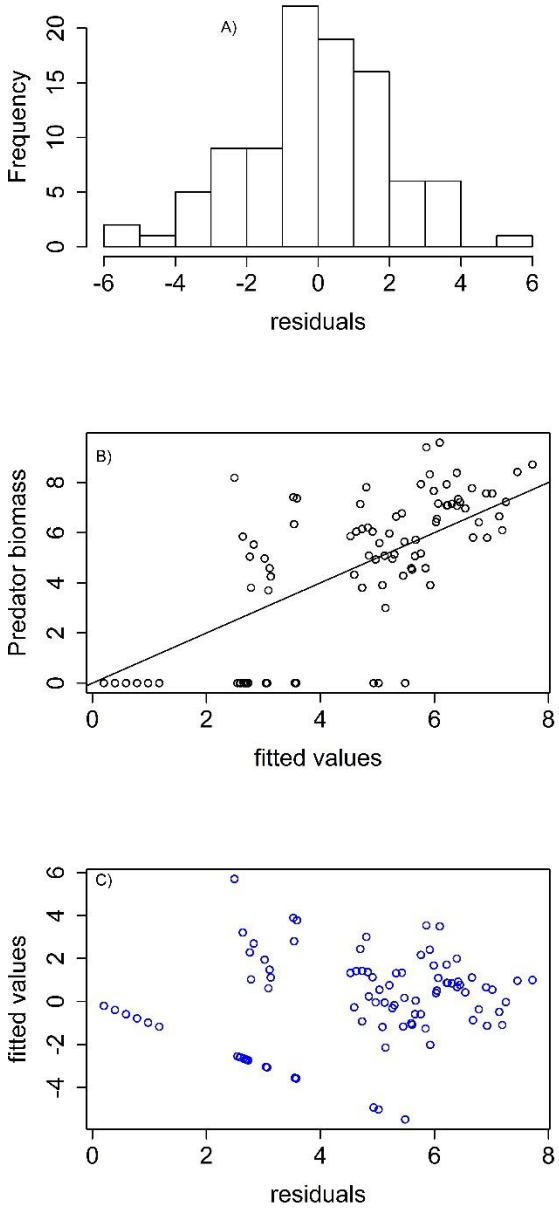
Appendix Figure 5. The model fit of the mixed effect model Equation 3a, regressing the $\log_2$ abundance of predators, defined using the narrow level of predator, each year against mean-centred year. The model residuals are normally distributed (A), but the fitted values do not predict the actual empirical values well (B), and there is evidence of heteroscedasticity (C). These issues are likely a product of the 0 abundances for the two predators who presence defines narrow predation levels.



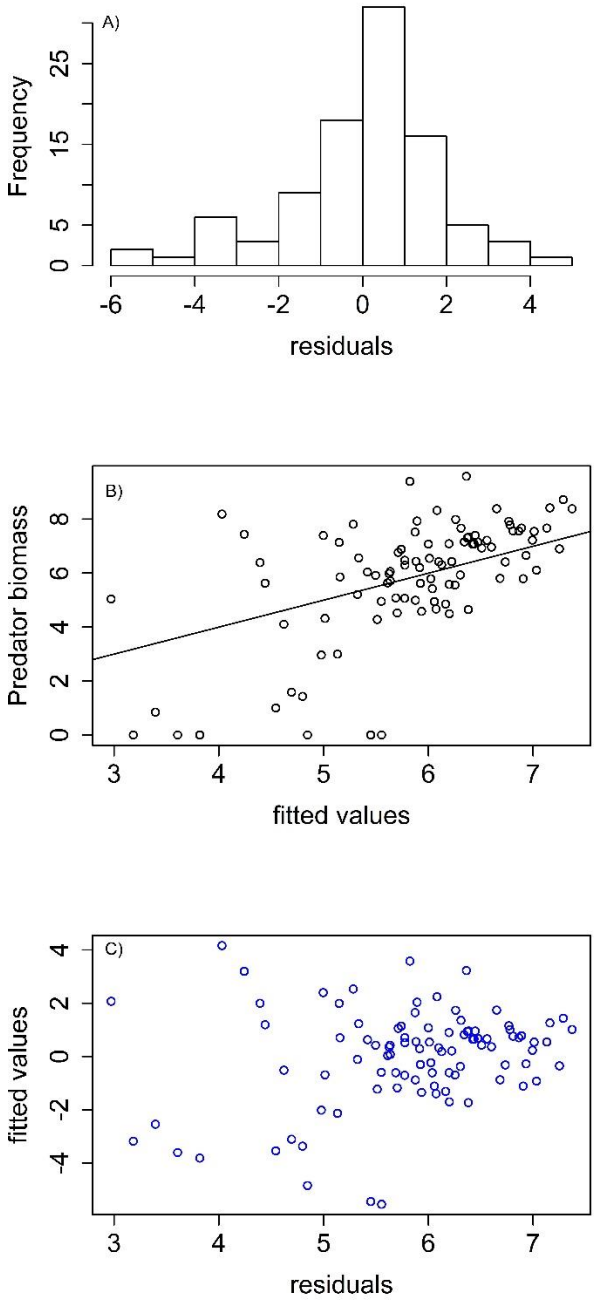
Appendix Figure 6. The model fit of the mixed effect model Equation 3b, regressing the $\log_2$ abundance of predators, defined using the intermediate level of predator, each year against mean-centred year. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity(C).



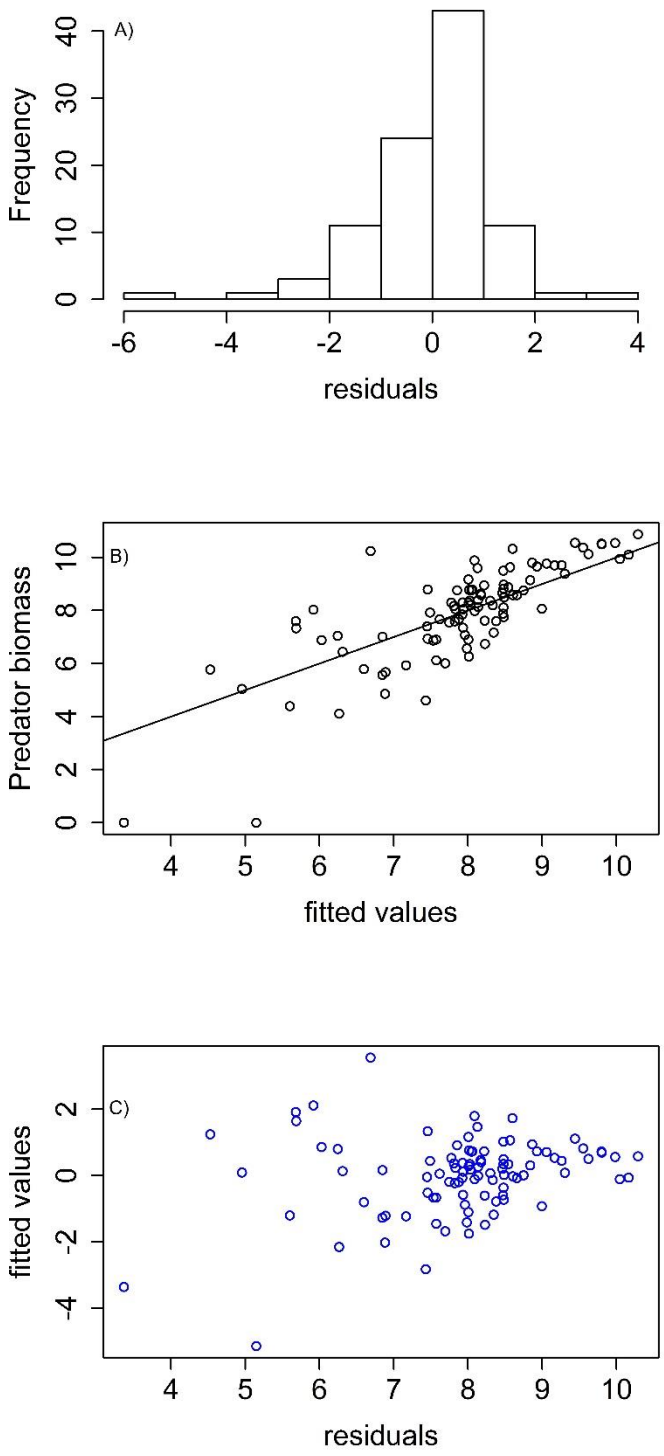
Appendix Figure 7. The model fit of the mixed effect model Equation 3c, regressing the $\log_2$ abundance of predators, defined using the broad level of predator, each year against mean-centred year. The model residuals are mostly normally distributed (A), the fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).



Appendix Figure 8. The model fit of the mixed effect model Equation 3d, regressing the $\log_2$ biomass of predators, defined using the wide level of predator, each year against mean-centred year. The model residuals are normally distributed (A), but the fitted values do not predict the actual empirical values well (B), and there is evidence of heteroscedasticity (C). These issues are likely a product of the 0 abundances for the two predators who presence defines narrow predation levels.



Appendix Figure 9. The model fit of the mixed effect model Equation 3e, regressing the $\log_2$ biomass of predators, defined using the intermediate level of predator, each year against mean-centred year. The model residuals are somewhat normally distributed, although shifted to the right (A). The fitted values do not predict the actual empirical values well (B), although there is no evidence of heteroscedasticity (C).



Appendix Figure 10. The model fit of the mixed effect model Equation 3f, regressing the $\log_2$ biomass of predators, defined using the broad level of predator, each year against mean-centred year. The model residuals are somewhat normally distributed, although shifted to the right (A). The fitted values do not predict the actual empirical values very well (B), although there is no evidence of heteroscedasticity (C).

Appendix Table 3. A list of all studies used in the Chapter 3 analysis.

These studies were sourced from the BioTIME database. This database is published as a data paper (Dornelas *et al*., 2018b) and can be access from http://biotime.st-andrews.ac.uk/home.php.

The column “ab or bio” refers to whether abundance was quantified in terms of numerical abundance (A), biomass (B) or both (AB).

Study ID	Realm	Climate	Taxa	Title	Number of years	Start year	End year	Central latitude	Central longitude	Number of Species	Total records	Ab or Bio	References
44	Terrestrial	Temperate	Terrestrial plants	Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3. 1962-Present	1962	1977	16	44.33	-122.33	158	25571	AB	C. B. Halpern, C. Dyrness, "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. **Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073**, accessed 2012. (2010). C. B. Halpern, J. A. Lutz, Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory–understory interactions.

													Ecological Monographs **83**, 221-237 (2013). C. B. Halpern, J. A. Lutz, "Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory–understory interactions". **Available at: Dryad DigitalRepository, doi:10.5061/dryad.1q88j**, accessed 2013 (2013).
56	Terrestrial	Temperate	Mammals	Small Mammal Mark-Recapture Population Dynamics at Core Research Sites	1989	2008	20	34.2	-106.43	28	16657	AB	M. Friggens, "Sevilleta LTER Small Mammal Population Data", Albuquerque, NM: Sevilleta Long Term Ecological Research Site Database: SEV008. **Available at: http://sev.lternet.edu/data/sev-8**, accessed 2012 (2008).

75	Marine	Polar	Marine invertebrates	Zooplankton Data from the Canadian Beaufort Sea Shelf. 1984 and 1985 NOGAP B2. Zooplankton Data from the Canadian Beaufort Sea Shelf. 1986. Central and Arctic Region	1985	1987	3	70.07606	-132.943	304	12643	AB	G. E. Hopky, M. J. Lawrence, D. B. Chiperzak, "Beaufort Sea NOGAP1 Zooplankton - NOGAP B1, Zooplankton Data from the Canadian Beaufort Sea Shelf, 1984-1985". Arctic Ocean Diversity, University of Alaska Fairbanks, Fairbanks. **Available at: http://www.arcodiv.org/Database/Plankton_datasets**, accessed 2012. G. E. Hopky, M. J. Lawrence, D. B. Chiperzak, "Beaufort Sea NOGAP2 Zooplankton - NOGAP B2, Zooplankton Data from the Canadian Beaufort Sea Shelf, 1987-1988". Arctic Ocean Diversity, University of Alaska Fairbanks, Fairbanks.

													Available at: http://www.arcodiv.org/Database/Plankton_datasets, accessed 2012. G. E. Hopky, M. J. Lawrence, D. B. Chiperzak, "Beaufort Sea NOGAP3 Zooplankton - NOGAP B3, Zooplankton Data from the Canadian Beaufort Sea Shelf, 1986". Arctic Ocean Diversity, University of Alaska Fairbanks, Fairbanks. **Available at: http://www.arcodiv.org/Database/Plankton_datasets**, accessed 2012.
86	Marine	Temperate	Marine plants	Phytoplankton of the Ukrainian Black Sea shelf (1985-2005)	1985	1998	14	44.68258	35.43957	368	9998	AB	N. Derezuyk, "Phytoplankton of the Ukrainian Black Sea shelf (1985-2005)". **Available at: http://www.emodnet-biology.eu/component/imis/?module=dataset&dasid=2**

													694, accessed 2012.
99	Marine	Temperate /Tropical	Fish	CSIRO Marine Data Warehouse (OBIS Australia)	1978	1997	20	-25.5979	134.0251	761	40884	B	T. Siferd, Central and Arctic Multi-Species Stock Assessment Surveys. OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada (OBIS Canada). **Available at: http://www.iobis.org/mapper/?dataset=2293**, accessed 2012 (2010).
119	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	1970	2010	41	43.98743	-63.6697	231	121804	AB	D. Clark, B. Branton, DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. *Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada*, (2007).
123	Marine	Temperate	Fish	Maine Department of Marine Resources	2000	2009	10	43.8912	-68.9407	144	36935	AB	S. Sherman, "Maine Department of Marine Resources

				Inshore Trawl Survey 2000?2009 (OBIS-USA)									Inshore Trawl Survey, 2000-2009". Maine Department of Marine Resources, Maine. **Available at: http://www.usgs.gov/obis-usa/data_search_and_access/datasets.html**, accessed 2012. (2010).
125	Marine	Temperate	Fish	MARMAP Chevron Trap Survey 1990-2009 (OBIS-USA)	1988	2000	13	31.44165	-78.8489	101	15092	AB	M. Reichert, "MARMAP Chevron Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources U.S.A. **Available at: http://www.usgs.gov/obis-usa/data_search_and_access/partici**

													pants.html, accessed 2012. (2009).
127	Marine	Temperate	Fish	MARMAP Florida Antillean Trap Survey 1990-2009 (OBIS-USA)	1980	1989	10	32.3347	-78.9923	48	4546	AB	M. Reichert, "MARMAP Florida Antillean Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources U.S.A. **Available at: http://www.usgs.gov/obis-usa/data_search_and_access/participants.html**, accessed 2012. (2009).
135	Marine	Temperate /Tropical	Fish	Previous_fisheries_REVIZEE_Program (Tropical and Subtropical	1972	1986	15	-13.0215	-45.1663	151	8468	B	REVIZEE, "Previous_fisheries_REVIZEE_Program", accessed through Tropical and Subtropical

				Western South Atlantic OBIS)									Western South Pacific OBIS. **Available at:** http://www.iobis.org/mapper/?dataset=2411, accessed 2012.
148	Marine	Temperate /Tropical	Fish	South Western Pacific Regional OBIS Data provider for the NIWA Marine Biodata Information System (South Western Pacific OBIS)	1964	2005	42	-42.407	172.26	430	351472	B	NIWA, "South Western Pacific Regional OBIS Data provider for the NIWA Marine Biodata Information System". Ocean Biogeographic Information System. Occurrence Dataset. **Available at:** https://doi.org/10.15468/zuuiyu, accessed 2012.
163	Marine	Temperate	Benthos	North Pacific Groundfish Observer (North Pacific Research Board)	1993	2004	12	56.5	-168.15	355	419940	AB	NPRB, "The Observer Program database", accessed through the OBIS-USA North Pacific Groundfish Observer (North Pacific Research Board). **Available at:** http://www.iobis.o

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176	Marine	Temperate	Marine invertebrates/plants	Atlantic Zone Monitoring Program Maritimes Region (AZMP) plankton datasets. In Fisheries and Oceans Canada - BioChem archive (OBIS Canada)	1998	2010	13	45.07336	-60.5645	320	56938	AB	M. Kennedy, J. Spry, Atlantic Zone Monitoring Program Maritimes Region plankton datasets. *Fisheries and Oceans Canada-BioChem archive. OBIS Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada*, (2011).
211	Marine	Temperate	Fish	MARMAP Fly Net 1990-2009	1980	1987	8	32.90096	-78.6855	127	1653	AB	M. Reichert, "MARMAP Fly Net 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources

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212	Marine	Temperate	Fish	MARMAP Yankee Trawl 1990-2009	1973	1980	8	31.94076	-78.8251	522	15532	AB	M. Reichert, "MARMAP Yankee Trawl 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate data surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources USA. **Available at: http://www.usgs.gov/obis-usa**, accessed 2013. (2010).
213	Marine	Temperate	Benthos	Northeast Fisheries Science Center Bottom Trawl Survey Data (OBIS-USA)	1948	2008	61	36.62513	-72.636	1023	439452	AB	NMFS, "Northeast Fisheries Science Center Bottom Trawl Survey Data (OBIS-USA)." NOAA's National Marine Fisheries Service (NMFS) Northeast

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232	Marine	Polar/Temperate	Fish	Pelagic Fish Observations 1968-1999	1968	1999	32	-56.8147	93.88436	185	6446	AB	D. Williams, "Pelagic Fish Observations 1968-1999." Australian Antarctic Data Centre. **Available at: http://www.gbif.org/dataset/85b0a82a-f762-11e1-a439-00145eb45e9a**, accessed 2012.
234	Terrestrial	Temperate	Terrestrial plants	Forest Inventory of a Northern Hardwood Forest Watershed 6	1982	2002	21	43.95347	-71.7396	15	4815	AB	J. J. Battles, Johnson, C., Hamburg, S., Fahey, T., Driscoll, C. & Likens, G., "Forest Inventory of a Northern Hardwood Forest: Watershed 6 2002." The Hubbard Brook Ecosystem Study

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													Ecosystem Study LTER Program. **Available at: http://www.hubbardbrook.org/data/dataset.php?id=31**, accessed 2016.
235	Terrestrial	Temperate	Terrestrial plants	Forest Inventory of a Northern Hardwood Forest Watershed 5?	1982	1999	18	43.95306	-71.7353	18	2823	AB	J. J. Battles, Fahey, T. & Cleavitt, N., "Forest Inventory of a Whole Tree Harvest: Hubbard Brook Experimental Forest Watershed 5, 1982, pre-harvest." The Hubbard Brook Ecosystem Study LTER Program. **Available at: http://www.hubbardbrook.org/data/dataset.php?id=36**, accessed 2012. (2003). J. J. Battles, Fahey, T. & Cleavitt, N., "Forest Inventory of a Whole Tree Harvest: Hubbard Brook Experimental Forest Watershed 5, 1990, 7 years post-harvest." The Hubbard Brook

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239	Terrestrial	Temperate	Terrestrial plants	Pinon Juniper Net Primary Production Quadrat Data from the Sevilleta National Wildlife Refuge New Mexico 1999-2001	1999	2001	3	34.35	-106.88	123	5288	AB	E. Muldavin, "Pinon Juniper Net Primary Production Quadrat Data from the Sevilleta National Wildlife Refuge, New Mexico: 1999-2001." Sevilleta Long Term Ecological Research Program. . **Available at: http://sev.lternet.edu/data/sev-187**, accessed 2013.
240	Terrestrial	Temperate	Terrestrial plants	Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta National Wildlife	2003	2015	13	34.35	-106.88	167	15561	AB	E. Muldavin, "Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta National Wildlife Refuge, New Mexico (2003-Present)." Sevilleta Long Term Ecological

				Refuge New Mexico (2003-present)									Research Program. **Available at: http://sev.lternet.edu/node/1718**, accessed 2013.
243	Terrestrial	Temperate	Terrestrial plants	Long-term N-fertilized vegetation plots on Hog Island Virginia Coastal Barrier Islands 1992 to 2014	1992	2014	23	37.44663	-75.6675	51	8508	AB	F. Day, "Long-term N-fertilized vegetation plots on Hog Island, Virginia Coastal Barrier Islands, 1992-2014." Virginia Coast Reserve Long-Term Ecological Research Project. **Available at: http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.106**, accessed 2013. (2010). F. P. Day, C. Conn, E. Crawford, M. Stevenson, Long-term effects of nitrogen fertilization on plant community structure on a coastal barrier island dune chronosequence. *Journal of Coastal Research*, 722-730 (2004).

247	Freshwater	Temperate	Freshwater invertebrates	Zooplankton survey of Oneida Lake New York 1964 to present	1975	2006	32	43.19662	-75.9198	31	30307	AB	L. Rudstam, "Zooplankton survey of Oneida Lake, New York, 1964 – 2012", KNB Data Repository. **Available at: https://knb.ecoinformatics.org/#view/kgordon.17.56**, accessed 2016. (2008).
252	Marine	Temperate	Fish	MARMAP Blackfish Trap Survey 1990-2009	1977	1989	13	32.45388	-78.9682	48	4692	AB	M. Reichert, "MARMAP Blackfish Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program. SCDNR MARMAP Aggregate Data Surveys. The Marine Resources Monitoring. Assessment. and Prediction (MARMAP) Program. Marine Resources Research Institute. South Carolina Department of Natural Resources USA. **Available at: http://www.usgs.gov/obis-usa/**,

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254	Freshwater	Temperate	Freshwater plants	North Temperate Lakes LTER Phytoplankton - Madison Lakes Area 1995 - current	1995	2014	20	43.08111	-89.3832	374	12652	AB	N. LTER, "North Temperate Lakes LTER: Phytoplankton - Madison Lakes Area 1995 - current." North Temperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison. **Available at: https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current**, accessed 2013.
275	Terrestrial	Temperate	Reptiles	Response of an urban remnant reptile community to summer wildfire	2009	2014	6	-31.9675	115.8333	19	1549	AB	R. A. Davis, T. S. Doherty, Rapid recovery of an urban remnant reptile community following summer wildfire. *PloS one* **10**, e0127925 (2015).

279	Terrestrial	Temperate	Terrestrial plants	Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3. 1962-Present	1979	2008	30	44.33	-122.33	261	27114	AB	C. B. Halpern, C. Dyrness, "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. **Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073**, accessed 2012. (2010). C. B. Halpern, J. A. Lutz, Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory–understory interactions. *Ecological Monographs* **83**, 221-237 (2013). C. B. Halpern, J. A. Lutz, "Canopy

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283	Marine	Polar	Marine invertebrates	Zooplankton Data from the Canadian Beaufort Sea Shelf. 1984 and 1985 NOGAP B2. Zooplankton Data from the Canadian Beaufort Sea Shelf. 1986. Central and Arctic Region	1985	1986	2	70.18796	-133.937	177	1720	B	G. E. Hopky, M. J. Lawrence, D. B. Chiperzak, "Beaufort Sea NOGAP2 Zooplankton - NOGAP B2, Zooplankton Data from the Canadian Beaufort Sea Shelf, 1987-1988". Arctic Ocean Diversity, University of Alaska Fairbanks, Fairbanks. **Available at: http://www.arcodiv.org/Database/Plankton_datasets**, accessed 2012. G. E. Hopky, M. J. Lawrence, D. B. Chiperzak,

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284	Marine	Temperate /Tropical	Fish	Previous_fisheries_REVIZEE_Program (Tropical and Subtropical Western South Atlantic OBIS)	1972	1986	15	-11.2057	-43.617	136	5906	AB	REVIZEE, "Previous_fisheries_REVIZEE_Program", accessed through Tropical and Subtropical Western South Pacific OBIS. **Available at: http://www.iobis.org/mapper/?dataset=2411**, accessed 2012.
286	Marine	Temperate	Fish	Maine Department of Marine Resources Inshore Trawl Survey	2000	2009	10	43.89725	-68.9221	29	883	B	S. Sherman, "Maine Department of Marine Resources Inshore Trawl Survey, 2000-

				2000?2009 (OBIS-USA)									2009". Maine Department of Marine Resources, Maine. **Available at: http://www.usgs.gov/obis-usa/data_search_and_access/datasets.html**, accessed 2012. (2010).
289	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	1995	2010	16	43.98438	-63.3485	68	452	B	D. Clark, B. Branton, DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. *Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada*, (2007).
290	Marine	Temperate /Tropical	Fish	CSIRO Marine Data Warehouse (OBIS Australia)	1978	1995	18	-25.813	135.2776	915	25494	AB	CMAR, "CSIRO Marine Data Warehouse - OBIS Australia", CSIRO Division of Marine and Atmospheric Research (CMAR), Australia. **Available at http://www.iobis.org**, accessed 2012.

293	Terrestrial	Temperate	Terrestrial plants	Rothamsted Parkgrass Experiment	1858	1976	119	51.80957	-0.35632	36	1124	B	Rothamsted, "Rothamsted Park Grass Experiment. Over 100 years of Park Grass" Accessed 2016.
295	Marine	Temperate	Fish	Systematic global assessment of reef fish communities by the Reef Life Survey program	2008	2016	9	-33.0513	139.1838	450	25469	AB	G. J. Edgar, R. D. Stuart-Smith, Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* **1**, 140007 (2014).
298	Terrestrial	Temperate	Terrestrial plants	Long-term mapped quadrats from Kansas prairie demographic information for herbaceaous plants	1903	1972	70	38.8	-99.3	146	147201	B	P. B. Adler, W. R. Tyburczy, W. K. Lauenroth, Long-term mapped quadrats from Kansas prairie: demographic information for herbaceaous plants. *Ecology* **88**, 2673-2673 (2007).
308	Terrestrial	Temperate	Mammals	Powdermill Nature Reserve monitored small mammal populations	1979	1999	21	40.17074	-79.2602	14	35398	AB	J. Merritt, Long Term Mammal Data from Powdermill Biological Station 1979-1999. Environmental Data Initiative. **Available at:**

				from 1979-1999.									http://dx.doi.org/10.6073/pasta/83c888854e239a79597999895bb61cfe, accessed 2016 (1999).
314	Terrestrial	Temperate	Mammals	Successional Dynamics on a Resampled Chronosequence Small mammal abundance	1983	1985	3	45.4	-93.2	6	118	A	J. Knops, D. Tilman, Successional Dynamics on a Resampled Chronosequence - Experiment 014. Cedar Creek Ecosystem Science Reserve. . Available at http://www.cedarcreek.umn.edu/research/data/dataset?ghe014, accessed 2016.
316	Terrestrial	Temperate	Reptiles	Lizard pitfall trap data (LTER-II LTER-III)	1989	2006	18	32.62	-106.74	21	2650	AB	D. Lightfoot, "Lizard pitfall trap data (LTER-II, LTER-III)". Jornada Basin LTER. Available at: http://jornada.nmsu.edu/lter/dataset/49821/view, accessed 2016. (2013).
320	Terrestrial	Temperate	Birds	Bird community dynamics in	1986	2015	30	43.91	-71.75	30	959	A	R. Holmes, F. Sturges, Bird community

				a temperate deciduous forest Long-term trends at Hubbard Brook									dynamics and energetics in a northern hardwoods ecosystem. *The Journal of Animal Ecology*, 175-200 (1975). R. T. Holmes, T. W. Sherry, Assessing population trends of New Hampshire forest birds: local vs. regional patterns. *The Auk*, 756-768 (1988). R. T. Holmes, T. W. Sherry, Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *The Auk* **118**, 589-609 (2001). R. T. Holmes, T. W. Sherry, F. W. Sturges, Bird Community Dynamics in a Temperate Deciduous Forest: Long-Term Trends at Hubbard Brook.

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321	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study. Jornada LTER. SMES rodent trapping data	1995	2007	13	32.55034	-106.812	19	12787	AB	D. Lightfoot, R. L. Schooley, "SMES rodent trapping data, Small Mammal Exclosure Study". Jornada LTER. **Available at: http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/data_files/JornadaStudy_086_smes_rodent_trapping_data_0.csv**, accessed 2016.
327	Terrestrial	Temperate	Mammals	Fray Jorge Small Mammals 1989-2005	1989	2005	17	-30.6	-71.7	12	256469	AB	D. Kelt, P. Meserve, J. Gutiérrez, W. B. Milstead, M. Previtali, Long-term monitoring of mammals in the face of biotic and abiotic influences at a semiarid site in north-central Chile. *Ecology* **94**, 977-977 (2013).
334	Terrestrial	Polar	Terrestrial plants	Above ground plant biomass in a mesic acidic	1982	2000	19	68.62964	-149.576	40	14003	B	M. C. Mack, E. A. Schuur, M. S. Bret-Harte, G. R. Shaver, F. S. Chapin, Ecosystem

				tussock tundra experimental site from 1982 to 20000 Toolik lake Alaska									carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**, 440-443 (2004). G. Shaver, "Above ground plant biomass a moist acidic tussock tundra experimental site, 1984, Artic LTER, Toolik Lake, Alaska". **Available at: http://dx.doi.org/10.6073/pasta/08a91cb2697f7cdc82d654e82b53c5c5**, accessed 2016. (2015). G. R. Shaver, F. S. Chapin, Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs* **61**, 1-31 (1991).

348	Terrestrial	Temperate /Tropical	Mammals	Bats (Mammalia Chiroptera) in restinga in the municipality of Jaguaruna south of Santa Catarina Brazil.	2006	2016	11	-28.6089	-48.9813	13	177	AB	F. Carvalho, J. J. Zocche, R. Á. Mendonça, Morcegos (Mammalia, Chiroptera) em restinga no município de Jaguaruna, sul de Santa Catarina, Brasil. *Biotemas* **22**, 193-201 (2009).
349	Marine	Temperate	Benthos	St. M polychaete species time-series	1991	2011	21	34.91799	-123.026	141	1730	AB	C. Laguionie-Marchais *et al.*, Inter-annual dynamics of abyssal polychaete communities in the North East Pacific and North East Atlantic—A family-level study. *Deep Sea Research Part I: Oceanographic Research Papers* **75**, 175-186 (2013). C. Laguionie-Marchais, G. L. Paterson, B. J. Bett, K. L. Smith, H. A. Ruhl, Inter-annual species-level variations in an abyssal polychaete

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350	Marine	Temperate	Benthos	Megafauna PAP time series	1989	2011	23	49	-16.5	50	563	AB	D. Billett, B. Bett, W. Reid, B. Boorman, I. Priede, Long-term change in the abyssal NE Atlantic: The 'Amperima Event'revisited. *Deep Sea Research Part II: Topical Studies in Oceanography* **57**, 1406-1417 (2010). D. Billett *et al.*, Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Progress in Oceanography* **50**, 325-348 (2001).
351	Marine	Temperate	Benthos	Megafauna Sta M time series	1989	2004	16	34.833 33	-123	10	350	AB	L. A. Kuhnz, H. A. Ruhl, C. L. Huffard, K. L. Smith, Rapid changes and long-term cycles in the benthic

													megafaunal community observed over 24years in the abyssal northeast Pacific. *Progress in Oceanography* **124**, 1-11 (2014). H. A. Ruhl, K. L. Smith, Shifts in deep-sea community structure linked to climate and food supply. *Science* **305**, 513-515 (2004).
354	Marine	Temperate /Tropical	Marine plants	A database of marine phytoplankton abundance biomass and species composition in Australian waters	1928	2015	88	-39.9788	129.9031	734	75604	AB	C. H. Davies *et al.*, A database of marine phytoplankton abundance, biomass and species composition in Australian waters. *Scientific data* **3**, (2016).
355	Terrestrial	Temperate	Terrestrial plants	Plant Species Composition on Selected Watersheds at Konza Prairie	1983	2015	33	39.08333	-96.5833	324	580983	B	D. C. Hartnett, S. L. Collins, PVC02 Plant Species Composition on Selected Watersheds at Konza Prairie. Environmental

													Data Initiative. **Available at: http://dx.doi.org/10.6073/pasta/7b6df00de4d0fcecfd344c02de9f9c62**, accessed 2017 (2016).
360	Terrestrial	Temperate	Birds	Bialowieza National Park bird assemblage	1975	2014	40	52.71667	24.26666	86	10061	AB	L. Tomiałojć, T. Wesołowski, Structure of a primaeval forest bird community during 1970s and 1990s (Białowieża National Park, Poland). *Acta Ornithologica* **31**, 133-154 (1996). L. Tomiałojć, T. Wesołowski, Die Stabilität der Vogelgemeinschaft in einem Urwald der gemässigten Zone: Ergebnisse einer 15jährigen Studie aus dem Nationalpark von Białowieża (Polen). *Beob* **91**, 73-110 (1994). L. Tomiałojć, T. Wesołowski, W. Walankiewicz, Breeding bird

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370	Marine	Temperate	Marine plants	Monitoring site 1000 coastal zone research - Algae survey permanent quadrats	2008	2014	7	36.7008	137.2608	159	2917	B	Monitoring Site 1000 Project, Biodiversity Center, M. o. E. o. Japan, "Monitoring site 1000 Coastal zone research - Algae survey".

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371	Marine	Temperate	Marine plants	Monitoring site 1000 coastal zone research - Algae survey transects	2008	2014	7	36.7054	137.2646	168	2887	B	Monitoring Site 1000 Project, Biodiversity Center, M. o. E. o. Japan, "Monitoring site 1000 Coastal zone research - Algae survey". **(MOB02.zip, downloaded from http://www.biodic.go.jp/moni1000/findings/data/index_file_algalbeds.html)**, Accessed 2016. (2015).
375	Terrestrial	Temperate	Terrestrial invertebrates	Surface of the earth wandering beetles survey data	2004	2014	11	36.24489	136.9066	424	19937	AB	Monitoring Site 1000 Project, Biodiversity Center, M. o. E. o. Japan, "Monitoring site 1000 Forest and grassland research - Surface wandering beetles survey data". **(GBDataPackage2014ver1.zip, downloaded from http://www.biodic.go.jp/moni1000/fi**

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383	Terrestrial	Temperate	Terrestrial plants	Boubin	1972	2010	39	48.97761	13.81091	9	24	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
384	Terrestrial	Temperate	Terrestrial plants	Cahnov-Soutok	1973	2006	34	48.65524	16.94116	14	40	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
385	Terrestrial	Temperate	Terrestrial plants	Milesice	1972	2011	40	48.98471	13.83861	5	14	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
386	Terrestrial	Temperate	Terrestrial plants	Mionsi-V	1994	2009	16	49.53636	18.66028	6	12	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at:

													http://naturalforests.cz/research. accessed 2016.
387	Terrestrial	Temperate	Terrestrial plants	Mionsi-R	1958	2009	52	49.53775	18.66117	4	12	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
388	Terrestrial	Temperate	Terrestrial plants	Mionsi-C	1957	2014	58	49.53611	18.65453	5	15	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
389	Terrestrial	Temperate	Terrestrial plants	Ranspurk	1973	2006	34	48.67882	16.94816	20	49	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
390	Terrestrial	Temperate	Terrestrial plants	Razula	1972	2009	38	49.35979	18.38194	8	18	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic".

													Available at: http://naturalforests.cz/research. accessed 2016.
391	Terrestrial	Temperate	Terrestrial plants	Salajka	1974	2007	34	49.40188	18.41952	6	18	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
392	Terrestrial	Temperate	Terrestrial plants	Stozec	1974	2013	40	48.87972	13.83582	10	29	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
393	Terrestrial	Temperate	Terrestrial plants	Velka Ples	1976	2013	38	49.98962	13.80339	15	40	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
394	Terrestrial	Temperate	Terrestrial plants	Zakova hora	1974	2011	38	49.65469	15.9905	10	26	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech

													Republic". Available at: http://naturalforests.cz/research. accessed 2016.
395	Terrestrial	Temperate	Terrestrial plants	Zofin	1975	2008	34	48.66659	14.70682	9	24	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
396	Terrestrial	Temperate	Terrestrial plants	Doutnac	2006	2016	11	49.95532	14.15337	22	44	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
397	Terrestrial	Temperate	Terrestrial plants	Polednik	2002	2010	9	50.86183	15.15315	6	11	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
398	Terrestrial	Temperate	Terrestrial plants	Polom	1973	1995	23	49.78985	15.7522	16	31	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of

													the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
399	Terrestrial	Temperate	Terrestrial plants	V Kluci	1973	2000	28	49.31325	15.52292	8	15	AB	T. Vrška, K. Král, D. Janík, D. Adam, "Natural Forests of the Czech Republic". Available at: http://naturalforests.cz/research. accessed 2016.
407	Marine	Temperate	Fish	Conicyt-Fondecyt Fish Data	2012	2013	2	-31.3206	-71.4224	15	293	AB	S. D. Ling *et al.*, Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **370**, (2014). A. R. Pérez-Matus, C. S. , Conicyt-Fondecyt Fish and Turf Algae Data", Chile, Subtidal Ecology Laboratory, Estacion Costera de Investigaciones Marinas, Facultad

													de Ciencias Biológicas. **Pontificia Universidad Catolica de Chile**, accessed 2016.
408	Marine	Temperate	Marine invertebrates	Conicyt-Fondecyt Turf Algae Data	2012	2013	2	-31.4159	-71.5589	18	1113	B	(S. D. Ling *et al.*, Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **370**, (2014). A. R. Pérez-Matus, C. S. , Conicyt-Fondecyt Fish and Turf Algae Data", Chile, Subtidal Ecology Laboratory, Estacion Costera de Investigaciones Marinas, Facultad de Ciencias Biológicas. **Pontificia Universidad Catolica de Chile**, accessed 2016.
409	Marine	Temperate	Fish	Conicyt-Fondecyt Fish Data	2012	2013	2	-31.4159	-71.5589	20	798	AB	S. D. Ling *et al.*, Global regime shift dynamics of

													catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **370**, (2014). A. R. Pérez-Matus, C. S. , Conicyt-Fondecyt Fish and Turf Algae Data", Chile, Subtidal Ecology Laboratory, Estacion Costera de Investigaciones Marinas, Facultad de Ciencias Biológicas. **Pontificia Universidad Catolica de Chile**, accessed 2016.
410	Marine	Temperate /Tropical	Fish	Conicyt-Fondecyt Fish Data	2014	2014	1	-31.001	-71.65	11	164	AB	S. D. Ling *et al.*, Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **370**, (2014).

													A. R. Pérez-Matus, C. S. , Conicyt-Fondecyt Fish and Turf Algae Data", Chile, Subtidal Ecology Laboratory, Estacion Costera de Investigaciones Marinas, Facultad de Ciencias Biológicas. **Pontificia Universidad Catolica de Chile**, accessed 2016.
411	Marine	Temperate /Tropical	Marine invertebrates	Conicyt-Fondecyt turf Algae Data	2014	2014	1	-31.001	-71.65	11	197	B	S. D. Ling *et al.*, Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **370**, (2014). A. R. Pérez-Matus, C. S. , Conicyt-Fondecyt Fish and Turf Algae Data", Chile, Subtidal Ecology Laboratory, Estacion Costera de Investigaciones Marinas, Facultad

													de Ciencias Biológicas. **Pontificia Universidad Catolica de Chile**, accessed 2016.
417	Terrestrial	Temperate	Terrestrial plants	Spatial and Temporal Patterns of Net Primary Production in Chihuahuan Desert Ecosystems	1989	2012	24	32.62	-106.74	329	173109	B	L. F. Huenneke, D. Clason, E. Muldavin, Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* **47**, 257-270 (2001). D. Peters, J. Anderson, "Spatial and Temporal Patterns of Net Primary Production in Chihuahuan Desert Ecosystems (NPP Study)", Jornada Basin LTER. **Available at: http://jornada.nmsu.edu/content/npp-study-quadrat-biomass-data**, accessed 2016.
426	Freshwater	Temperate	Freshwater	Phytoplankton time	1976	2010	35	47.33	8.56	64	2082	B	F. Pomati, B. Matthews, J.

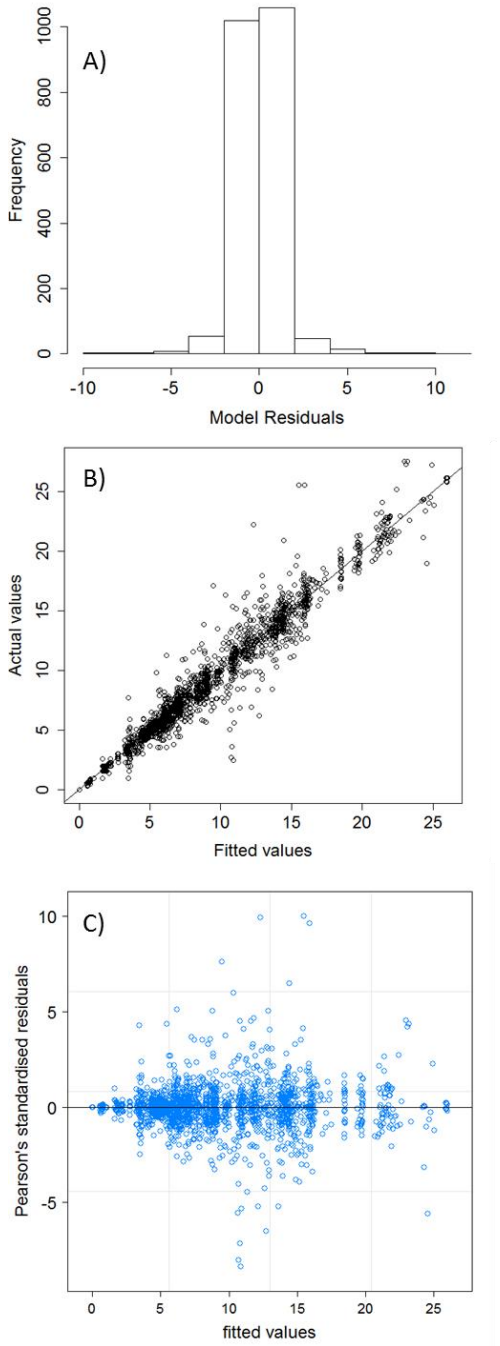
			invertebrates	series from Lake Zurich									Jokela, A. Schildknecht, B. W. Ibelings, Effects of re-oligotrophication and climate warming on plankton richness and community stability in a deep mesotrophic lake. *Oikos* **121**, 1317-1327 (2012). F. Pomati *et al.*, Challenges and prospects for interpreting long-term phytoplankton diversity changes in Lake Zurich (Switzerland). *Freshwater Biology* **60**, 1052-1059 (2015).
427	Freshwater	Temperate	Freshwater invertebrates	Zooplankton time series from Lake Zurich	1977	2008	32	47.33	8.56	65	4819	AB	F. Pomati, B. Matthews, J. Jokela, A. Schildknecht, B. W. Ibelings, Effects of re-oligotrophication and climate warming on plankton richness and community stability in a deep

													mesotrophic lake. *Oikos* **121**, 1317-1327 (2012). F. Pomati *et al.*, Challenges and prospects for interpreting long-term phytoplankton diversity changes in Lake Zurich (Switzerland). *Freshwater Biology* **60**, 1052-1059 (2015).
435	Marine	Polar/Temperate	Marine invertebrates	Zooplankton collected with a 2-m 700-um net towed from surface to 120 m aboard Palmer Station Antarctica LTER annual cruises off the western antarctic peninsula 2009 - present	2009	2016	8	-67.0946	-70.9793	40	5187	AB	D. Steinberg, Zooplankton collected with a 2-m, 700-um net towed from surface to 120 m, aboard Palmer Station Antarctica LTER annual cruises off the western antarctic peninsula, 2009 - 2016. Environmental Data Initiative. **Available at: http://dx.doi.org/10.6073/pasta/fb658789188724be5f27c81a634647d5**, accessed 2017 (2017).

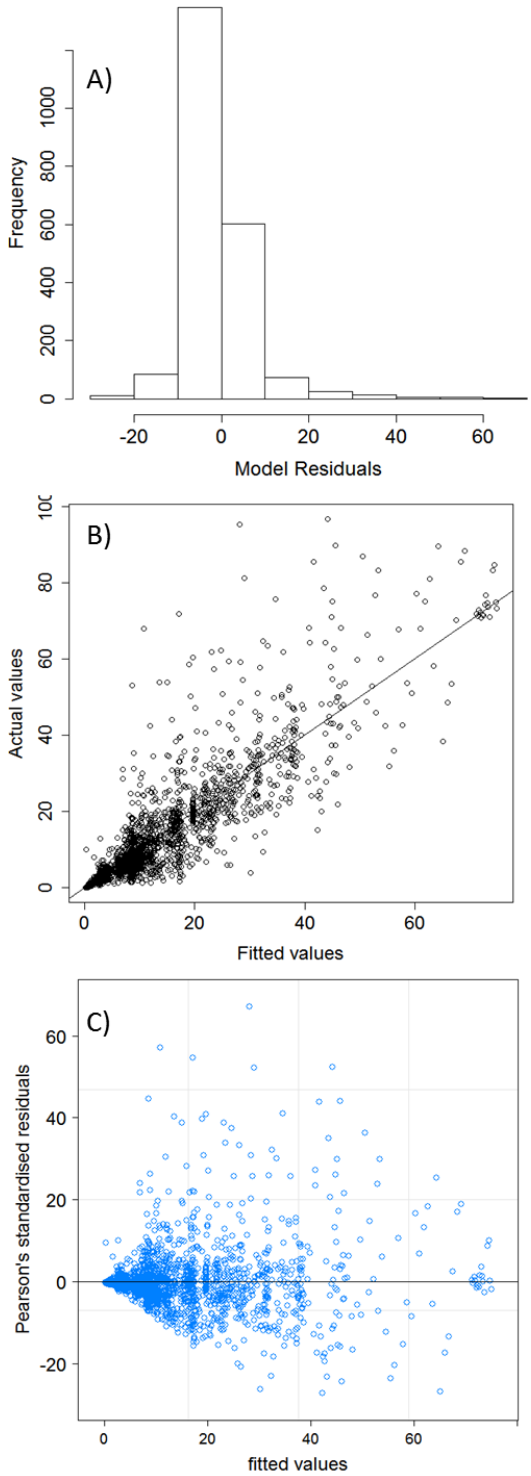
436	Marine	Tropical	Fish	Karimunjawa WCS fish survey	2005	2012	8	-5.81932	110.3625	394	34176	AB	A. Hoey, "Karimunjawa WCS fish data". Accessed 2016.
437	Marine	Tropical	Fish	Aceh WCS fish survey 2010 to 2016	2010	2016	7	5.753012	95.27988	188	2340	AB	A. Hoey, "Aceh WCS fish 2010-16". Accessed 2016.
438	Marine	Tropical	Fish	Aceh WCS fish surveys	2006	2014	9	5.764892	95.21924	598	35263	AB	A. Hoey, "Aceh WCS fish surveys". Accessed 2016.
450	Marine	Temperate	Fish	Composition (%) and biomass (thous. tons) of fish species in Olyutorsky-Navarin area in 2005-2012	2005	2012	8	60.23333	168.35	26	103	B	G. M. G. Gavrilov, I. A., The composition and community structure of benthic fish in the economic zone of Russia Bering sea on the results of studies of "TINRO centre" in 2005-2012 years. *Modern problems of science and education* **11**, 37–49. (2013).
451	Marine	Temperate	Fish	Composition (%) and biomass (thous. tons) of fish species in Gulf of	2005	2012	8	64	-178	20	78	B	G. M. G. Gavrilov, I. A., The composition and community structure of benthic fish in the economic zone of Russia Bering sea on the results of

				Anadyr in 2005-2012									studies of “TINRO centre” in 2005-2012 years. *Modern problems of science and education* **11**, 37–49. (2013).
452	Marine	Temperate	Fish	Year-to-year dynamics of total nekton biomass (thous. tons) in the upper epipelagic of the North-West Pacific in June-July of 2000s	2004	2012	9	47	160	13	100	B	A. Khoruzhiy, S. Naydenko, Species structure and year-to-year dynamics of nekton biomass in the upper epipelagic layer of the Pacific waters at Kuril Islands in summer periods of the 2000s. *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr* **176**, 16-36 (2014).
453	Freshwater	Polar/Temperate	Freshwater invertebrates	Population dynamics of some species founded in all periods of study in the lake Bolshoi Kharbei in late July - early August (thous.individuals/m3)	1969	2010	42	67.33	62.53	15	42	A	E. B. Fefilova *et al.,* Long-Term Changes of Aquatic Communities in the Kharbeyskie Lakes. *Journal of Siberian Federal University. Biology* **7**, 240 (2014).

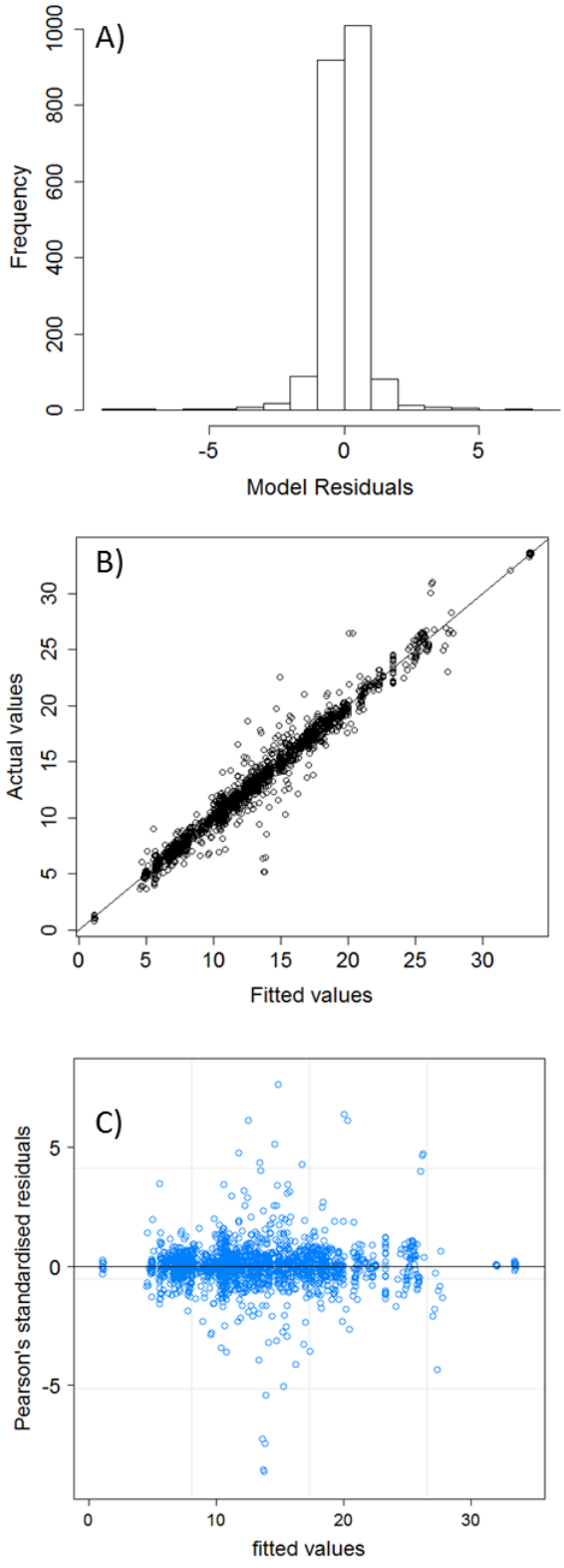
Appendix Chapter 4



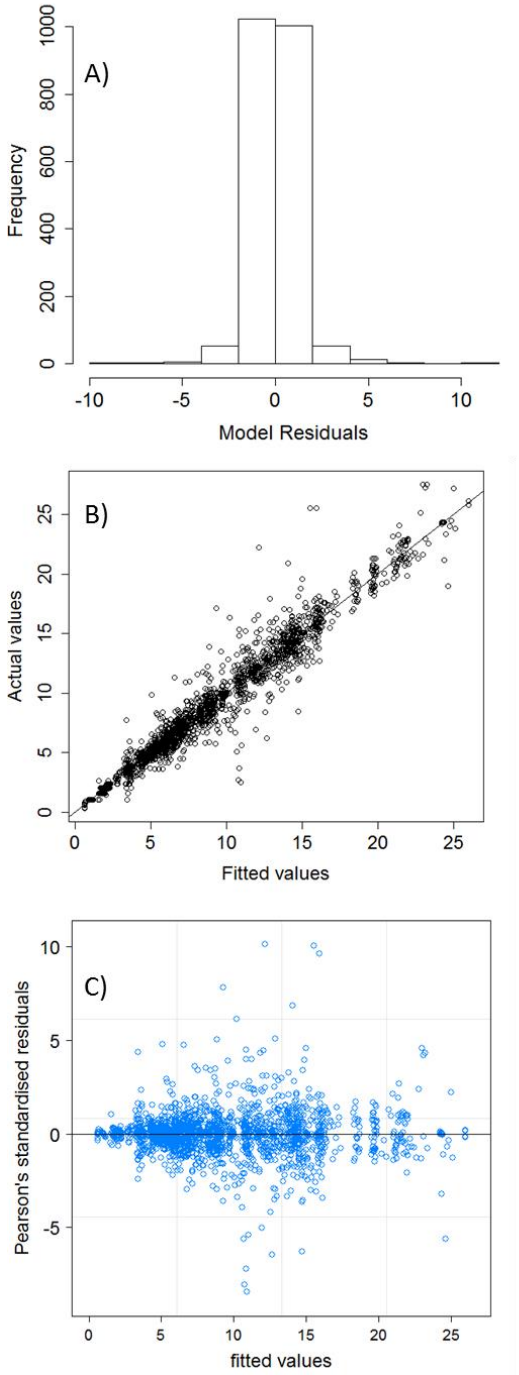
Appendix Figure 11. The model fit of the mixed effect model Equation 4a of log_2 absolute dominance change against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



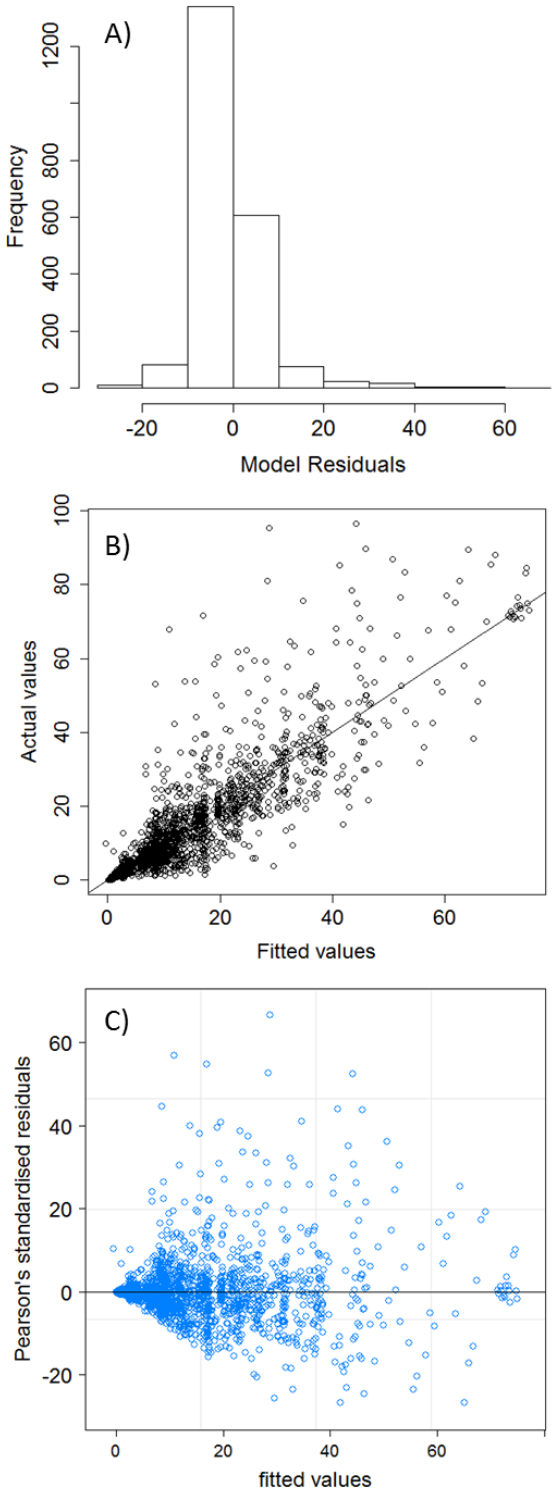
Appendix Figure 12. The model fit of the mixed effect model Equation 4b of relative (%) dominance change against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



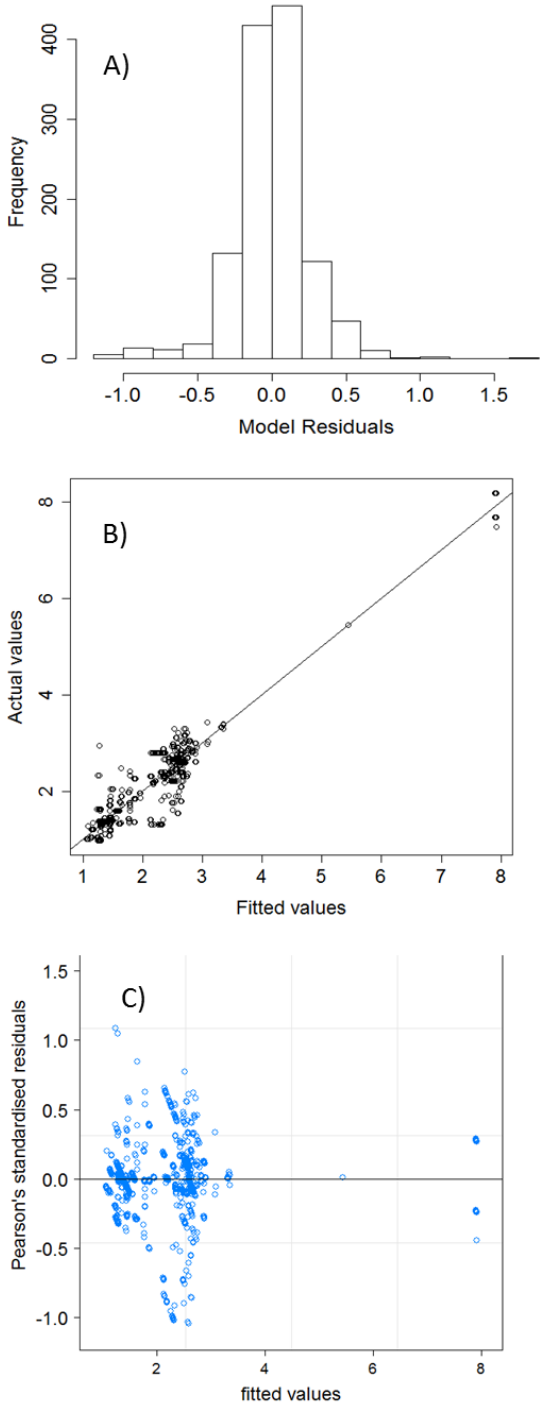
Appendix Figure 13. The model fit of the mixed effect model Equation 5 of $\log_2$ assemblage size change (measured in numerical abundance) against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



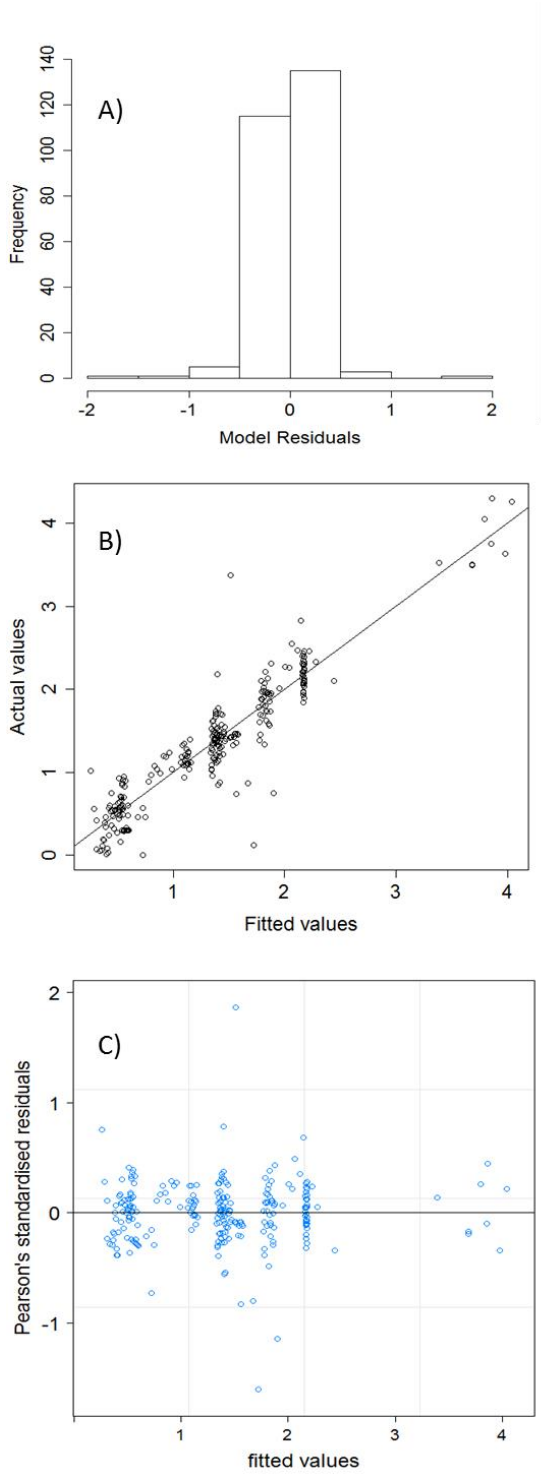
Appendix Figure 14. The model fit of the mixed effect model Equation 6a of $\log_2$ absolute dominance change against mean-centred year. The model residuals are mostly normally distributed (A). The fitted values predict the actual empirical values (B), but there is more error around these predictions than in Appendix Figure 1(B).There is also evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data reasonably well, I decided to use this model structure despite the heteroscedasticity.



Appendix Figure 15. The model fit of the mixed effect model Equation 6b of relative (%) dominance change against mean-centred year. The model residuals are mostly normally distributed, but there is a left skew (A). The fitted values predict the actual empirical values (B), but there is more error around these predictions than in Appendix Figure 1(B).There is also evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data reasonably well, I decided to use this model structure despite the heteroscedasticity.



Appendix Figure 16. The model fit of Equation 7, the mixed model of average vertebrate dominant species size (log_2) change regressed against mean centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence in plot (B) and (C) that large values may be overly affecting the model fit. These data refer to cetacean body size.



Appendix Figure 17. The model fit of Equation 8, which is the mixed model of dominant fish species average body size each year regressed against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is also no evidence of heteroscedasticity (C).

Appendix Table 3. A list of all studies used in the Chapter 4 analysis.

These studies were sourced from the BioTIME database. This database is published as a data paper (Dornelas *et al*., 2018b) and can be access from http://biotime.st-andrews.ac.uk/home.php

Study ID	Realm	Climate	Taxa	Title	Number of years	Start year	End year	Central latitude	Central longitude	Number of Species	Total records	Reference
18	Terrestrial	Temperate	Terrestrial plants	Mapped quadrats in sagebrush steppe long-term data for analyzing demographic rates and plant to plant interactions	29	1923	1973	44.33	-112.33	98	8034	Zachmann L, Moffet C, Adler P. Mapped quadrats in sagebrush steppe: long‐term data for analyzing demographic rates and plant‐plant interactions. Ecology. 2010;91(11):3427.
33	Marine	Temperate	Marine plants	Long-term phytoplankton community dynamics in the Western English Channel	18	1992	2009	50.25	-4.217	170	35676	Widdicombe CE, Eloire D, Harbour D, Harris RP, Somerfield PJ. Long-term phytoplankton community dynamics in the Western English Channel. J Plankton Res. 2010;fbp127
39	Terrestrial	Temperate	Birds	Bird community dynamics in a temperate deciduous forest Long-term trends at Hubbard Brook	45	1970	2015	43.91	-71.75	52	959	Holmes RT, Sherry TW, Sturges FW. Bird Community Dynamics in a Temperate Deciduous Forest: Long‐Term Trends at Hubbard Brook. Ecol Monogr. 1986;56(3):201‐20.
41	Terrestrial	Temperate	Birds	Time and space and the variation of species	10	1923	1940	39.5	-82.48	56	418	Preston FW. Time and space and the variation of species. Ecology. 1960;41(4):611–27.
42	Terrestrial	Temperate	Birds	Eastern Wood	30	1949	1979	51.2965	-0.38352	45	954	Beven G. Changes in breeding bird populations of an oak-wood on Bookham Common, Surrey, over twenty-seven years. London Nat. 1976;55:23–42.
44	Terrestrial	Temperate	Terrestrial plants	Plant succession and biomass dynamics following logging and burning in	16	1962	1977	44.33	-122.33	158	25571	Halpern CB, Dyrness C. “Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-

				the Andrews Experimental Forest Watersheds 1 and 3. 1962-Present								Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. 2010;Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073:accessed 2012.
46	Terrestrial	Temperate	Birds	Skokholm Bird Observatory	47	1928	1979	51.698	-5.277	29	528	Vickery WL, Nudds TD. Detection of Density‐Dependent Effects in Annual Duck Censuses. Ecology. 1984;65(1):96–104.
47	Terrestrial	Temperate	Birds	Detection of Density-Dependent Effects in Annual Duck Censuses	26	1952	1977	50.845447	-107.446257	13	392	Vickery WL, Nudds TD. Detection of Density‐Dependent Effects in Annual Duck Censuses. Ecology. 1984;65(1):96–104.
51	Terrestrial	Temperate	Birds	Fluctuations and long-term in the relative densities of tetraonid populations in Finland. 1964-77	14	1964	1977	61.9241	25.7482	4	56	Lindén H, Rajala P. Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. Finnish Game Res. 1981;39:13–34.
52	Terrestrial	Polar	Mammals	A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish forest Lapland over 13 winters	13	1968	1980	67.75	29.5	3	144	Pulliainen E. A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. Ann Zool Fennici. 1981;270–8.
53	Terrestrial	Temperate	Mammals	An 11-year study of small mammal populations at Mont St. Hilaire. Quebec	10	1966	1976	45.564	-73.179	5	44	Grant PR. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. Can J Zool. 1976;54(12):2156–73.

54	Terrestrial	Tropical	Terrestrial invertebrates	El Verde Grid invertebrate data (Big Grid Snail Captures 1991-2007)	24	1991	2014	18.1667	-65.5	19	21702	Willig C. P. MR& B. "El Verde Grid long-term invertebrate data: Luquillo Long Term Ecological Research Site Database: Data Set 107." 2016;Available at:http://luq.lternet.edu/data/luqmetadata107/7427:accessed 2016. Available from: http://sev.lternet.edu/data/sev-187
56	Terrestrial	Temperate	Mammals	Small Mammal Mark-Recapture Population Dynamics at Core Research Sites	20	1989	2008	34.2	-106.43	28	16657	Friggens, M. (2008) "Sevilleta LTER Small Mammal Population Data", Albuquerque, NM: Sevilleta Long Term Ecological Research Site Database: SEV008. Available at: http://sev.lternet.edu/data/sev-8, accessed 2012.
57	Freshwater	Temperate	Fish	North Temperate Lakes LTER Fish Abundance	32	1981	2012	43.9928	-89.4946	76	10892	LTER NTL. "NTLFI02 North Temperate Lakes LTER: Fish Abundance 1981 - current". North Temperate Lakes Long Term Ecological Research program, NSF. Center for Limnology, University of Wisconsin-Madison. Available at: https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-fish-abundance-1981-current:accessed 2012.
58	Terrestrial	Tropical	Birds	Avian populations long-term monitoring dataset. San Juan. Puerto Rico Luquillo Long Term Ecological	18	1991	2008	18.19	-65.43	31	1171	Waide RB. "Bird abundance - point counts. El Verde Field Station, Puerto Rico: Luquillo Long Term Ecological Research Site Database: Data Set 23." 2010;Available at: http:/luq.lter

				Research Site Database Grid points bird counts DBAS 23								net.edu/data/luqmetadata23: accessed 2012.
59	Terrestrial	Temperate	Mammals	Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal. Arizona. USA	26	1977	2002	30.3226	-103.501	29	427	Ernest SK, Valone TJ, Brown JH. Long‐term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology. 2009;90(6):1708.
63	Terrestrial	Temperate	Terrestrial invertebrates	The development of dragonfly communities and the consequences of territorial behaviour A 27-year study on small ponds at Woodwalton Fen. Cambridgeshire. United Kingdom	29	1959	1988	52.4221	-0.180928	5	132	Moore NW. The development of dragonfly communities and the consequences of territorial behaviour: a 27 year study on small ponds at Woodwalton Fen, Cambridgeshire, United Kingdom. Odonatologica. 1991;20(2):203–31
67	Terrestrial	Temperate	Birds	Animal Demography Unit - Coordinated Waterbird Counts (CWAC) (AfrOBIS)	24	1983	2006	-28.954467	24.950961	68	15448	"Animal Demography Unit - Coordinated Waterbird Counts (CWAC) - AfrOBIS". . Available at: http://www.iobis.org/mapper/?dataset=603:accessed 2012.
70	Terrestrial	Temperate	Terrestrial invertebrates	Belgian Migrating Lepidoptera	14	1983	1996	51	4	25	303	Vanholder B. "Belgian Migrating Lepidoptera". NERC Centre for Population Biology, Imperial College. The Global Population Dynamics Database v2.0. . 1997;Available at: https://www.imperial.ac.uk/c

												pb/gpdd2/secure/register.aspx:accessed 2012.
78	Marine	Temperate	Benthos	IOW Macrozoobenthos monitoring Baltic Sea (1980-2005) (EurOBIS)	25	1980	2005	56.729642	18.236359	212	3587	Zettler ML. Macrozoobenthos baltic sea (1980-2005) as part of the IOW-Monitoring. Institut für Ostseeforschung Warnemünde, Germany. 2005;Available at: http://www.iobis.org/mapper/?dataset=2289:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=2289
81	Marine	Temperate	Mammals	CRRU Cetacean sighting in Scotland waters 1997-2010	14	1997	2010	57.767014	-2.642995	9	1613	Robinson KP. "CRRU (Cetacean Research and Rescue Unit) Cetacean sightings in Scotland waters." 2010;Available at: http://www.emodnet-biology.eu/component/imis/?module=dataset&dasid=2819:accessed 2012.
85	Marine	Temperate	Marine invertebrates	North Sea observations of Crustacea. Polychaeta. Echinodermata. Mollusca and some other groups between 1986 and 2003	12	1992	2003	53.604782	4.248107	354	9984	Addinck W, de Kluijver M. North Sea observations of Crustacea, Polychaeta, Echinodermata, Mollusca and some other groups between 1986 and 2003. Expert Centre for Taxonomic Idenditification (ETI), the Netherlands. 2003;Available at: http://www.emodnet-biology.eu/data-catalog?module=dataset&dasid=1037:accessed 2012.
97	Marine	Polar/Temperate	Marine invertebrates	Archives of the Arctic Seas Zooplankton (ARC)	22	1921	1973	72.739441	10.694448	402	15016	Markhaseva EL, Golikov AA, Agapova TA, Beig AA. Archives of the Arctic Seas Zooplankton. 1985;Available at:

												http://www.iobis.org/mapper/?dataset=4470:accessed 2012.
100	Marine	Temperate	Fish	Community level response to climate change The long-term study of the fish and crustacean community of the Bristol Channel	31	1981	2011	51.14	-3.08	83	5199	Henderson PA. The long-term study of the fish and crustacean community of the Bristol Channel. Available at http://www.pisces-conservation.com/:accessed 2013.
101	Marine	Temperate	Marine invertebrates	Community level response to climate change The long-term study of the fish and crustacean community of the Bristol Channel	31	1981	2011	51.14	-3.08	15	2210	Henderson PA. The long-term study of the fish and crustacean community of the Bristol Channel. Available at http://www.pisces-conservation.com/:accessed 2013.
108	Marine	Global	Birds	Seabirds of the Southern and South Indian Ocean (Australian Antarctic Data Centre)	29	1977	2006	-27.17355	3.945813	123	116226	Woehler E. “Seabirds of the Southern and South Indian Ocean - Australian Antarctic Data Centre.” Available at: http://www.iobis.org:accessed 2012.
112	Marine	Temperate/Tropical	Fish	NOAA Southeast Fishery Science Center (SEFSC) Commercial Pelagic Observer Program (POP) Data (SEFSC_POP)	22	1973	2005	24.981493	-51.374069	540	466437	"South Western Pacific Regional OBIS Data Asteroid Subset", NIWA (National Institute of Water and Atmospheric Research - New Zealand) MBIS (Marine Biodata Information System) accessed through South Western Pacific OBIS. Available at: http://www.iobis.org/mapper/?dataset=219, accessed 2012.

117	Marine	Temperate	Marine invertebrates	South Western Pacific Regional OBIS Data Asteroid Subset (South Western Pacific OBIS)	44	1956	2003	-39.371733	3.081897	156	2253	"South Western Pacific Regional OBIS Data Asteroid Subset", NIWA (National Institute of Water and Atmospheric Research - New Zealand) MBIS (Marine Biodata Information System) accessed through South Western Pacific OBIS. Available at: http://www.iobis.org/mapper/?dataset=219:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=219
119	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	41	1970	2010	43.987425	-63.669701	231	121804	Clark D, Branton B. DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. Bedford Inst Oceanogr Dartmouth, Nov Scotia, Canada, OBIS Canada. 2007;
125	Marine	Temperate	Fish	MARMAP Chevron Trap Survey 1990-2009 (OBIS-USA)	12	1988	2000	31.441647	-78.848859	101	15092	Reichert M. "MARMAP Chevron Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources U.S.A. 2009;Available at: http://www.usgs.gov/obis-usa/data_search_and_access/participants.html:accessed 2012.

152	Marine	Temperate	Marine invertebrates	CMarZ (Census of Marine Zooplankton)-Asia Database	15	1977	2002	43.855961	3.065693	163	2493	"CMarZ (Census of Marine Zooplankton)-Asia Database". Accessed through OBIS- SCAR-MarBIN. Available at: http://www.iobis.org/mapper/?dataset=1500:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=1500
163	Marine	Temperate	Benthos	North Pacific Groundfish Observer (North Pacific Research Board)	12	1993	2004	56.5	-168.15	355	419940	"The Observer Program database", accessed through the OBIS-USA North Pacific Groundfish Observer (North Pacific Research Board). Available at: http://www.iobis.org:accessed 2012.
166	Marine	Global	All	PIROP Northwest Atlantic 1965-1992 (SEAMAP)	25	1965	1992	36.075242	-70.991806	213	155600	"PIROP Northwest Atlantic 1965-1992 - OBIS SEAMAP". Available at: http://www.iobis.org/mapper/?dataset=2245:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=2245
169	Marine	Temperate	All	CalCOFI and NMFS Seabird and Marine Mammal Observation Data. 1987-2006 (SEAMAP)	20	1987	2006	34.858456	-121.614941	185	61730	Jahncke C. J& R. "CalCOFI and NMFS Seabird and Marine Mammal Observation Data, 1987-2006". California Cooperative Oceanic Fisheries Investigations (CalCOFI) and National Marine Fisheries Service (NMFS) cruises, 1987-2006 - OBIS SEAMAP. 2006;Available at: http://www.iobis.org:accessed 2012.
172	Marine	Temperate	All	POPA cetacean. seabird. and sea turtle sightings in	12	1998	2009	35.009739	-24.224698	47	52291	"POPA cetacean, seabird, and sea turtle sightings in the Azores area 1998-2009 - OBIS

				the Azores area 1998-2009 (OBIS SEAMAP)								SEAMAP". . Available at: http://www.iobis.org/mapper/?dataset=4257:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=4257
176	Marine	Temperate	Marine invertebrates	Atlantic Zone Monitoring Program Maritimes Region (AZMP) plankton datasets. In Fisheries and Oceans Canada - BioChem archive (OBIS Canada)	13	1998	2010	45.073359	-60.564453	320	56938	Kennedy MK, Spry JA. Atlantic Zone Monitoring Program Maritimes Region plankton datasets. Fish Ocean Canada-BioChem Arch OBIS Canada, Bedford Inst Oceanogr Dartmouth, Nov Scotia, Canada. 2011;
180	Marine	Polar/Temperate	Fish	ECNASAP - East Coast North America Strategic Assessment (OBIS Canada)	26	1970	1995	37.770564	-50.792666	273	410802	"East Coast North America Strategic Assessment Project, Groundfish Atlas for the East Coast of North America." Available at: http://www.iobis.org:accessed 2012.
182	Marine	Temperate	All	Snow crab research trawl survey database (Southern Gulf of St. Lawrence. Gulf region. Canada) from 1988 to 2010 (OBIS Canada)	22	1988	2009	47.480915	-62.76169	33	35005	Wade EJ. Snow crab research trawl survey database (Southern Gulf of St. Lawrence, Gulf region, Canada) from 1988 to 2010. OBIS Canada, Bedford Inst Oceanogr Dartmouth, Nov Scotia, Canada. 2011;
183	Marine	Temperate	Marine invertebrates	DFO Maritimes Research Vessel Trawl Surveys Invertebrate Observations (OBIS Canada)	13	1999	2011	43.776648	-63.751421	16	14906	Wade EJ. Snow crab research trawl survey database (Southern Gulf of St. Lawrence, Gulf region, Canada) from 1988 to 2010. OBIS Canada, Bedford Inst

												Oceanogr Dartmouth, Nov Scotia, Canada. 2011;
190	Marine	Tropical	Fish	St. Croix. USVI Fish Assessment and Monitoring Data (2002 - Present) (NOAA-CCMA)	10	2001	2010	17.756969	-64.604258	247	28017	Wade EJ. Snow crab research trawl survey database (Southern Gulf of St. Lawrence, Gulf region, Canada) from 1988 to 2010. OBIS Canada, Bedford Inst Oceanogr Dartmouth, Nov Scotia, Canada. 2011;
191	Marine	Temperate	Marine invertebrates	NEFSC Benthic Database (OBIS-USA)	28	1900	1975	39.123056	-66.64136	1614	51456	"NEFSC Benthic Database (OBIS-USA)", Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Department of Commerce. 2010;Available at: http://www.iobis.org/mapper/?dataset=1694:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=1694
192	Marine	Polar/Temperate	Mammals	Whale Catches in Southern Ocean (OBIS - Australian Antarctic Data Centre)	42	1932	1980	-62.076411	79.717188	6	7122	"Whale Catches in Southern Ocean". OBIS - Australian Antarctic Data Centre. Available at: http://www.iobis.org:accessed 2013.
193	Marine	Temperate	Marine invertebrates	Community level response to climate change The long-term study of the fish and crustacean community of the Bristol Channel (plankton)	29	1982	2011	51.14	-3.08	7	775	Henderson PA. The long-term study of the fish and crustacean community of the Bristol Channel. Available at http://www.pisces-conservation.com/:accessed 2013.

195	Terrestrial	Temperate	Birds	Breeding birds survey North America	30	1978	2007	40.809241	-96.187269	385	699449	USGS Patuxent Wildlife Research Center "North American Breeding Bird Survey" ftp data set, version 2014.0. Available at: ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/:accessed 2013.
196	Marine	Temperate	Benthos	SOTEAG Rocky Shore Survey (Sullom Voe)	35	1976	2012	60.466447	-1.322878	252	91491	Moore JJ, Howson CM. "Survey of the rocky shores in the region of Sullom Voe, Shetland, A report to SOTEAG from Aquatic Survey & Monitoring Ltd", Cosheston, Pembrokeshire. 29 p. Available at: http://www.soteag.org.uk:accessed 2013.
197	Marine	Temperate	Fish	Scottish West Coast Surveys - all species of fish (1985 - 2013)	28	1985	2013	56.521156	-6.528952	149	279726	DATRAS. ICES Scottish West Coast Survey For Commercial Fish Species 1985-2013. 2013;Available at https://datras.ices.dk:accessed 2014. Available from: https://datras.ices.dk
198	Marine	Temperate	Fish	Baltic international demersal trawl surveys	23	1991	2013	56.359496	16.421731	142	751021	DATRAS. ICES Baltic International Trawl Survey For Commercial Fish Species (1991 - 2013). 2013;Available at https://datras.ices.dk:accessed 2013.
200	Marine	Temperate	Marine invertebrates	NEFSC Benthic Database (OBIS-USA)	30	1956	1989	35.691706	-74.090761	2105	102143	"NEFSC Benthic Database (OBIS-USA)", Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Department of Commerce. 2010;Available at: http://www.iobis.org/mapper

												/?dataset=1694:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=1694
204	Marine	Temperate	Benthos	MACROBEL Long term trends in the macrobenthos of the Belgian Continental Shelf	19	1976	2001	51.439215	2.682711	344	15901	Degraer Wittoeck, J., Appeltans, W., Cooreman, K., Deprez, T., Hillewaert, H., Hostens, K., Mees, J., Vanden Berghe, E. & Vincx, M. S. "Macrobel: Long term trends in the macrobenthos of the Belgian Continental Shelf." Oostende, Belgium. 2006;Available at: http://www.emodnet-biology.eu/data-catalog?module=dataset&dasid=145:accessed 2013.
206	Marine	Temperate	Fish	Northern Irish Ground Fish Trawl Survey	16	1993	2008	52.175977	-4.628473	108	13547	DATRAS. "Fish trawl survey: Northern Irish Ground Fish Trawl Survey. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2764:accessed 2013.
208	Marine	Temperate	Fish	ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)	11	1997	2007	48.521775	-6.248979	189	24867	DATRAS. "Fish trawl survey: ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-

												catalog?%3Fmodule=dataset &dasid=2759:accessed 2013.
209	Marine	Temperate	Fish	ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS) -UK	18	1990	2007	51.09476	0.085737	115	19711	DATRAS. "Fish trawl survey: ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset &dasid=2761:accessed 2013.
210	Marine	Temperate	Fish	ICES North Sea International Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)	47	1965	2011	56.463779	3.500367	254	296524	DATRAS. "Fish trawl survey: ICES North Sea International Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset &dasid=2763:accessed 2013.
213	Marine	Temperate	Benthos	Northeast Fisheries Science Center Bottom Trawl Survey Data (OBIS-USA)	48	1948	2008	36.625131	-72.635974	1023	439452	"NEFSC Benthic Database (OBIS-USA)", Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Department of Commerce. 2010;Available at: http://www.iobis.org/mapper/?dataset=1694:accessed 2012. Available from: http://www.iobis.org/mapper/?dataset=1694

214	Terrestrial	Temperate	Terrestrial plants	Long-term growth mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest 1910 to present	88	1910	2010	45.34296	-122.799	39	37350	Harmon J. M& F. "Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present." Long-Term Ecological Research. Forest Science Data Bank, Corvallis. 2012;Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TV010:accessed 2012.
215	Terrestrial	Temperate/Tropical	Birds	Hawk Migration Association of North America (HMANA)	57	1952	2008	38.40865	-99.515743	39	991769	HMANA. "Hawk Migration Association of North America (HMANA)." Available at: http://www.hmana.org/:accessed 2012.
217	Terrestrial	Temperate	Birds	Landbird Monitoring Program (UMT-LBMP)	14	1992	2006	46.828888	-109.981603	268	336516	USFS "Landbird Monitoring Program (UMT-LBMP)." US Forest Service. Available at: http://www.avianknowledge.net/:accessed 2012.
219	Terrestrial	Temperate	Amphibians	Marsh Monitoring Program - Amphibian Surveys	17	1995	2011	44.900466	-84.776848	14	41914	Bird Studies Canada (2012) "Marsh Monitoring Program." NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
220	Terrestrial	Temperate	Birds	Marsh Monitoring Program - Bird Surveys	17	1995	2011	46.885476	-80.033171	243	144779	Bird Studies Canada (2012) "Marsh Monitoring Program." NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
221	Terrestrial	Temperate	Terrestrial plants	Vegetation Plots of the Bonanza Creek LTER Control Plots	26	1975	2008	64.844229	-148.051765	52	1157	Viereck LA, Van Cleve K, Chapin FS, Ruess RW, Hollingsworth TN. Vegetation Plots of the Bonanza Creek

				Species Count (1975 - 2004)								LTER Control Plots: Species Count (1975 - 2004). Environmental Data Initiative. 2005;Available at: http://dx.doi.org/10.6073/pasta/8dd0e1ac48e2f82b51adabfbd3c62ae2:accessed 2012.
225	Terrestrial	Temperate	Birds	Point count bird censusing long-term monitoring of bird distrubution and diversity in central Arizona-Phoenix period 2000 to 2011	12	2000	2011	33.43	-111.93	278	48841	Shochat E, Katti M, Warren P. "Point count bird censusing: long-term monitoring of bird distribution and diversity in central Arizona-Phoenix: period 2000 to 2011". Central Arizona-Phoenix Long-Term Ecological Research. Global Institute for Sustainability, Arizona State University. 2004;Available at: https://caplter.asu.edu/data/data-catalog/?id=46:accessed 2012.
229	Freshwater	Temperate	Fish	Upper Little Tennessee River Biomonitoring Program Database - LTWA Biomonitoring Database	26	1988	2013	35.138164	-83.385518	69	11184	McLarney WO, Meador J, Chamblee J. "Upper Little Tennessee River Biomonitoring Program Database." Coweeta Long Term Ecological Research Program. 2010;Available at: https://coweeta.uga.edu/dbpublic/dataset_details.asp?accession=4045:accessed 2012.
232	Marine	Polar/Temperate	Fish	Pelagic Fish Observations 1968-1999	25	1968	1999	-56.814716	93.88436	185	6446	Williams D. "Pelagic Fish Observations 1968-1999." Australian Antarctic Data Centre. Available at: http://www.gbif.org/dataset/85b0a82a-f762-11e1-a439-00145eb45e9a:accessed 2012.

236	Freshwater	Temperate	Fish	Fish population on selected watersheds at Konza Prairie - CFP012 - Konza fish population	12	1995	2006	39.0931	-96.5586	19	1169	Gido KB. "Fish population on selected watersheds at Konza Prairie - CFP01." Konza Prairie LTER Program. Available at: http://www.konza.ksu.edu/KNZ/pages/data/Knzdsdetail.aspx?datasetCode=CFP01:accessed 2012.
237	Freshwater	Temperate	Freshwater invertebrates	Madison Wisconsin Lakes Zooplankton 1976 - 1994 - old net	19	1976	1994	43.025171	-89.325378	89	10610	Lathrop R. "Madison Wisconsin Lakes Zooplankton 1976 - 1994." North Temperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison. 2000;Available at: http://lter.limnology.wisc.edu/dataset/madison-wisonsin-lakes-zooplankton-1976-1994:accessed 2013.
238	Freshwater	Temperate	Freshwater invertebrates	North Temperate Lakes LTER Zooplankton - Madison Lakes Area 1997 - current	20	1995	2014	43.0716	-89.3971	32	7331	LTER NTL. "North Temperate Lakes LTER: Zooplankton - Madison Lakes Area 1997 - current." North Temperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison. 2011;Available at: http://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-madison-lakes-area-1997-current:accessed 2013.
240	Terrestrial	Temperate	Terrestrial plants	Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta	13	2003	2015	34.35	-106.88	167	15561	Muldavin E. "Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta National Wildlife Refuge, New Mexico (2003-Present)." Sevilleta

				National Wildlife Refuge New Mexico (2003-present)								Long Term Ecological Research Program. Available at: http://sev.lternet.edu/node/1718:accessed 2013. Available from: http://sev.lternet.edu/node/1718
243	Terrestrial	Temperate	Terrestrial plants	Long-term N-fertilized vegetation plots on Hog Island Virginia Coastal Barrier Islands 1992 to 2014	22	1992	2014	37.446634	-75.667464	51	8508	Day F. "Long-term N-fertilized vegetation plots on Hog Island, Virginia Coastal Barrier Islands, 1992-2014." Virginia Coast Reserve Long-Term Ecological Research Project. 2010;Available at: http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.106:accessed 2013.
244	Marine	Temperate	Birds	British Columbia Coastal Waterbirds Survey	14	1999	2012	50.55543	-126.283603	243	219126	Bird Studies Canada (2012) "BC Coastal Waterbird Survey (2004)." NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
246	Marine	Temperate	Fish	Long-term monitoring dataset of fish assemblages impinged at nuclear power plants in northern Taiwan	15	2000	2014	25.244306	121.624306	335	3722	Chen H, Liao Y-C, Chen C-Y, Tsai J-I, Chen L-S, Shao K-T. Long-term monitoring dataset of fish assemblages impinged at nuclear power plants in northern Taiwan. Sci data. 2015;2:150071.
247	Freshwater	Temperate	Freshwater invertebrates	Zooplankton survey of Oneida Lake New York 1964 to present	32	1975	2006	43.196619	-75.919813	31	30307	Rudstam L. "Zooplankton survey of Oneida Lake, New York, 1964 – 2012", KNB Data Repository. 2008;Available at:

												https://knb.ecoinformatics.org/#view/kgordon.17.56:accessed 2016.
249	Terrestrial	Temperate	Terrestrial invertebrates	Resource specialists lead local insect community turnover associated with temperature - analysis of an 18-year full-seasonal record of moths and beetles	24	1992	2015	55.702512	12.558956	1427	31787	Thomsen PF, Jørgensen PS, Bruun HH, Pedersen J, Riis-Nielsen T, Jonko K, *et al*. Resource specialists lead local insect community turnover associated with temperature – analysis of an 18-year full-seasonal record of moths and beetles. J Anim Ecol [Internet]. 2016;85(1):251–61. Available from: http://dx.doi.org/10.1111/1365-2656.12452
252	Marine	Temperate	Fish	MARMAP Blackfish Trap Survey 1990-2009	13	1977	1989	32.453878	-78.968171	48	4692	Reichert M. "MARMAP Blackfish Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program. SCDNR MARMAP Aggregate Data Surveys. The Marine Resources Monitoring. Assessment. and Prediction (MARMAP) Program. Marine Resources Research Institute. South Carolina Department of Natural Resources USA. 2010;Available at: http://www.usgs.gov/obis-usa/:accessed 2013.
253	Freshwater	Temperate	Freshwater invertebrates	North Temperate Lakes LTER Zooplankton - Trout Lake Area 1982 - current	29	1986	2014	46.021392	-89.652932	133	30750	LTER NTL. "North Temperate Lakes LTER: Zooplankton - Trout Lake Area 1982 - current." NorthTemperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison. Available at:

												https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-trout-lake-area-1982-current:accessed 2013.
254	Freshwater	Temperate	Freshwater plants	North Temperate Lakes LTER Phytoplankton - Madison Lakes Area 1995 - current	20	1995	2014	43.08111	-89.383155	374	12652	LTER NTL. "North Temperate Lakes LTER: Phytoplankton - Madison Lakes Area 1995 - current." North Temperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison. Available at: https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current:accessed 2013.
256	Marine	Temperate	Fish	ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS) - The Netherlands	24	1987	2010	56.341379	2.672616	120	37250	DATRAS. "Fish trawl survey: ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2761:accessed 2013.
271	Marine	Temperate	Fish	Santa Barbara Coastal LTER	15	2000	2014	34.305653	-119.874919	62	6287	Reed DC. "SBC LTER: Reef: Kelp forest community dynamics: Fish abundance". Santa Barbara Coastal LTER. Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-17 doi:10.6073/pasta/e37ed291

												11b2fddffc08355252b8b8c7:accessed 2016.
272	Marine	Temperate	Marine invertebrates	Santa Barbara Coastal LTER	15	2000	2014	34.305542	-119.87585	36	5363	Reed DC. "SBC LTER: Reef: Kelp forest community dynamics: Invertebrate and algal density". Santa Barbara Coastal LTER. . Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-19 doi:10.6073/pasta/cd4cf864efecd69891dfe1d73b9ac9c3:accessed 2016
273	Marine	Temperate	Marine invertebrates	Santa Barbara Coastal LTER	15	2000	2014	34.305542	-119.87585	27	15498	Reed DC. "SBC LTER: Reef: Kelp forest community dynamics: Invertebrate and algal density". Santa Barbara Coastal LTER. . Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-19 doi:10.6073/pasta/cd4cf864efecd69891dfe1d73b9ac9c3:accessed 2016.
288	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	34	1970	2006	43.977389	-63.682015	195	19074	Tremblay JM, Branton B. DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. Bedford Inst Oceanogr Dartmouth, Nov Scotia, Canada, OBIS Canada [Internet]. 2007; Available from: http://www.iobis.org/mapper/?dataset=257
297	Marine	Tropical	Marine invertebrates	MCR LTERCoral Reef Long-term Population and Community Dynamics Other Benthic	11	2005	2015	-17.524634	-149.837295	13	2734	Carpenter R. "MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Other Benthic Invertebrates, ongoing since 2005". Moorea Coral Reef

				Invertebrates. ongoing since 2005								LTER, knb-lter-mcr.7.28. 2015;Available at: doi:10.6073/pasta/8e7b3a0c7a8bf315739921861cc79d10:accessed 2016.
300	Terrestrial	Temperate	Terrestrial invertebrates	Insect Populations via Sticky Traps at KBS-LTER (Kellogg Biological Station. MI)	25	1989	2013	42.408852	-85.383181	21	47798	Landis D, Gage S. Insect Populations via Sticky Traps at KBS-LTER. 2014;Available at: http://lter.kbs.msu.edu/datatables/67:accessed 2016. Available from: http://lter.kbs.msu.edu/datatables/67
301	Terrestrial	Temperate	Terrestrial invertebrates	Konza LTER grasshopper monitoring. Konza Prairie LTER. KS	25	1982	2013	39.106	-96.611	51	10470	Joern A. CGR02 Sweep Sampling of Grasshoppers on Konza Prairie LTER watersheds (1982-present). Environmental Data Initiative. 2016;Available at: http://dx.doi.org/10.6073/pasta/7060b2c244229a37e3bfc8c18f14ad02:accessed 2016.
305	Terrestrial	Temperate	Amphibians	Population estimates of Appalachian salamanders. Coweeta LTER	15	1976	1990	35	-83.5	4	60	Wiley RH. “Population estimates of Appalachian salamanders”. Coweeta LTER. Available at: http://coweeta.uga.edu/eml/1044.xml:accessed 2016.
306	Freshwater	Temperate	Reptiles	Edwin S. George Reserve Turtles. The Global Population Dynamics Database Version 2	16	1975	1992	42.457	-83.946	3	46	NERC. “The Global Population Dynamics Database Version 2”. Centre for Population Biology, Imperial College. 2010;Available at: http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html:accessed 2016.
308	Terrestrial	Temperate	Mammals	Powdermill Nature Reserve monitored small mammal	21	1979	1999	40.170741	-79.260178	14	35398	Merritt J. Long Term Mammal Data from Powdermill Biological Station 1979-1999. Environmental Data Initiative.

				populations from 1979-1999.								1999;Available at: http://dx.doi.org/10.6073/pasta/83c888854e239a79597999895bb61cfe:accessed 2016.
309	Terrestrial	Temperate	Terrestrial invertebrates	Monitoring the Abundance of Butterflies 1976-1985	10	1976	1985	53.132177	-2.177679	44	5694	Pollard E, Hall ML, Bibby TJ. Monitoring the Abundance of Butterflies 1976-1985. Research & survey in nature conservation. 1986;Available at: http://jncc.defra.gov.uk/page-2614:accessed 2016.
311	Terrestrial	Temperate	Mammals	Seasonal summary of numbers of small mammals on 14 LTER traplines in prairie habitats at Konza Prairie	33	1981	2013	39.083333	-96.583333	15	2458	Kaufman DW. Seasonal summary of numbers of small mammals on 14 LTER traplines in prairie habitats at Konza Prairie. Konza Prairie Long-Term Ecological Research. . Available at: http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza:accessed 2016. Available from: http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza
313	Terrestrial	Temperate	Terrestrial invertebrates	Successional Dynamics on a Resampled Chronosequence Core Old Field Grasshopper Sampling	18	1989	2006	45.4	-93.2	61	7958	Knops J, Tilman D. Successional Dynamics on a Resampled Chronosequence - Experiment 014. Cedar Creek Ecosystem Science Reserve. . Available at http://www.cedarcreek.umn.edu/research/data/dataset?ghe014:accessed 2016.

316	Terrestrial	Temperate	Reptiles	Lizard pitfall trap data (LTER-II LTER-III)	18	1989	2006	32.62	-106.74	21	2650	Lightfoot, D. "Small Mammal Exclosure Study (SMES)". Sevilleta Long Term Ecological Research Program. Available at: http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0, accessed 2016.
318	Terrestrial	Temperate	All	Karoo National Park Census Data	13	1994	2009	-32.23333	22.283333	25	229	SANParks. "Karoo National Park Census Data. 1994 - 2009." 2011;Available at: http://datadryad.org/handle/10255/dryad.13079?show=full:accessed 2016.
319	Terrestrial	Temperate	All	Effects of rangeland management on community dynamics of herpetofauna to the tallgrass prairie	14	1989	2003	37.25	-96.71666	35	232	Wilgers DJ, Horne EA, Sandercock BK, Volkmann AW. Effects of rangeland management on community dynamics of the herpetofauna of the tallgrass prairie. Herpetologica. 2006;62(4):378–88.
321	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study. Jornada LTER. SMES rodent trapping data	13	1995	2007	32.550335	-106.811564	19	12787	Lightfoot D. "Small Mammal Exclosure Study (SMES)". Sevilleta Long Term Ecological Research Program. Available at: http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0:accessed 2016.
327	Terrestrial	Temperate	Mammals	Fray Jorge Small Mammals 1989-2005	17	1989	2005	-30.6	-71.7	12	256469	Kelt, D. A., Meserve, P. L., Gutiérrez, J. R., Milstead, W. B. & Previtali, M. A. (2013) Long-term monitoring of mammals in the face of biotic and abiotic influences at a semiarid site in north-central Chile. Ecology, 94, 977. doi:10.1890/12-1811.1.

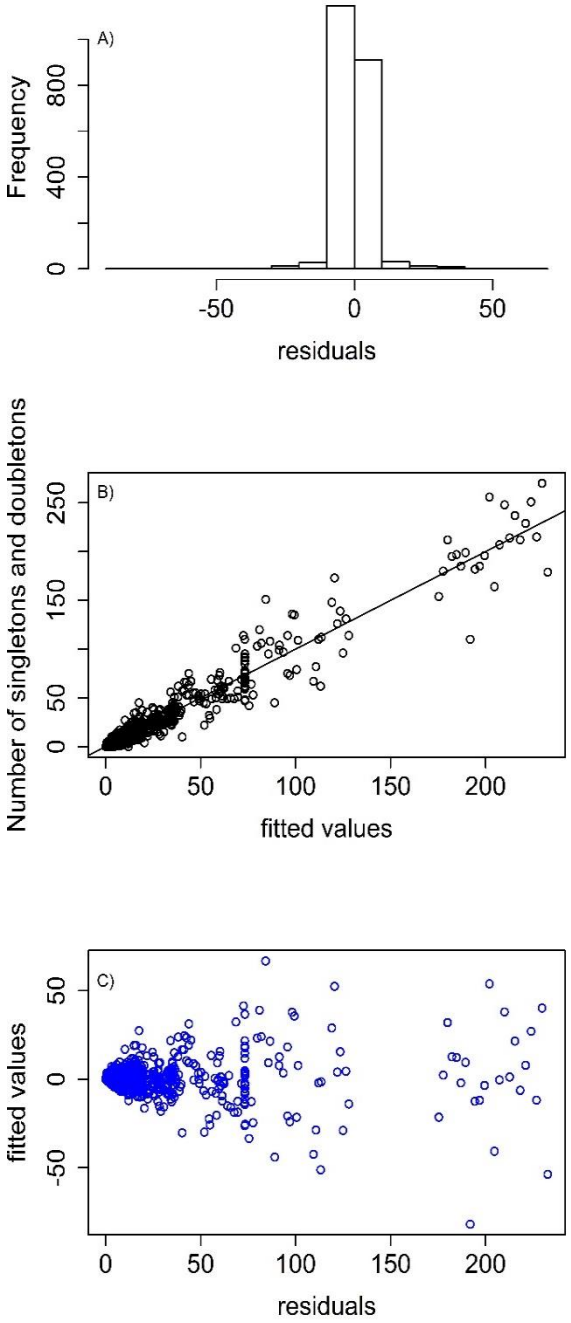
328	Freshwater	Temperate	Amphibians	The Rainbow Bay Long-term Study	30	1979	2008	32.26	-81.63	10	301	Scott D, Metts B, Lance S. "The Rainbow Bay Long-term Study." Available at: http://srelherp.uga.edu/projects/rbay.htm:accessed 2016.
330	Marine	Temperate/Tropical	Marine invertebrates	Over 75 years of zooplankton data from Australia	49	1938	2014	-23.830553	136.449216	639	80764	Davies CH, Armstrong AJ, Baird M, Coman F, Edgar S, Gaughan D, *et al*. Over 75 years of zooplankton data from Australia. Ecology. 2014;95(11):3229.
332	Freshwater	Temperate	Fish	Stream Fish Assemblage stability in a southern Appalachian stream (Coweeta Hydro Lab 1984 - 1995)	12	1984	1995	35.0589	-83.4319	14	590	Grossman GD. "Stream fish assemblage stability in a southern Appalachian stream at the Coweeta Hydrologic Laboratory from 1984 to 1995".
336	Terrestrial	Temperate	Terrestrial plants	Long term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal Arizona	14	1989	2002	31.938889	-109.0797	100	35978	Ernest SK, Valone TJ, Brown JH. Long‐term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology. 2009;90(6):1708.
339	Terrestrial	Temperate	Birds	Species trends turnover and composition of a woodland bird community in southern Sweden during a period of 57 years.	57	1953	2009	55.71667	13.33333	39	1210	Svensson S, Thorner AM, Nyholm NEI. Species trends, turnover and composition of a woodland bird community in southern Sweden during a period of fifty-seven years. Ornis Svecica. 2010;20(1):31–44.
340	Terrestrial	Temperate	Terrestrial plants	Small Mammal Exclosure Study	15	1995	2009	34.296	-106.9267	93	1608	Lightfoot D. "Small Mammal Exclosure Study (SMES) Vegetation Data from the

				(SMES) Vegetation Data from the Chihuahuan Desert								Chihuahuan Desert Grassland and Shrubland at the Sevilleta National Wildlife Refuge, New Mexico (2006-2009)". Long Term Ecological Research Network. 2011;Available at: http://dx.doi.org/10.6073/pasta/d80d5e2196cd11ef79df23ebe5a77c19:accessed 2016.
348	Terrestrial	Temperate/Tropical	Mammals	Bats (Mammalia Chiroptera) in restinga in the municipality of Jaguaruna south of Santa Catarina Brazil.	10	2006	2016	-28.6089	-48.98125	13	177	Carvalho, F., Zocche, J.J. & Mendonça, R.Á. (2009) Morcegos (Mammalia, Chiroptera) em restinga no município de Jaguaruna, sul de Santa Catarina, Brasil. Biotemas, 22, 193-201.
350	Marine	Temperate	Benthos	Megafauna PAP time series	12	1989	2011	49	-16.5	50	563	Billett, D., Bett, B., Rice, A., Thurston, M., Galéron, J., Sibuet, M. & Wolff, G. (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography, 50, 325-348. Billett, D., Bett, B., Reid, W., Boorman, B. & Priede, I. (2010) Long-term change in the abyssal NE Atlantic: The 'Amperima Event'revisited. Deep Sea Research Part II: Topical Studies in Oceanography, 57, 1406-1417.
351	Marine	Temperate	Benthos	Megafauna Sta M time series	13	1989	2004	34.833333	-123	10	350	Ruhl, H. A. & Smith, K. L. (2004) Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply. Science, 305, 513–515. Kuhnz, L. A., Ruhl, H. A., Huffard, C. L. & Smith, K. L.

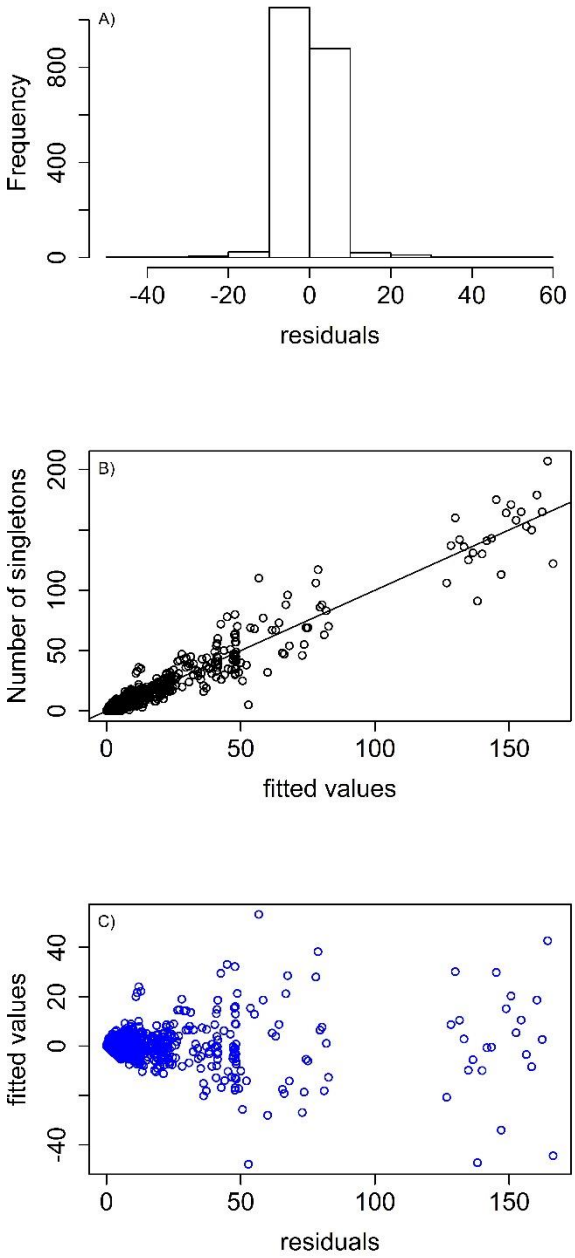
												(2014) Rapid changes and long-term cycles in the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific. Progress in Oceanography, 124, 1–11.
354	Marine	Temperate/Tropical	Marine plants	A database of marine phytoplankton abundance biomass and species composition in Australian waters	24	1928	2015	-39.978763	129.903106	734	75604	Davies CH, Coughlan A, Hallegraeff G, Ajani P, Armbrecht L, Atkins N, *et al*. A database of marine phytoplankton abundance, biomass and species composition in Australian waters. Sci data. 2016;3.
356	Terrestrial	Tropical	Terrestrial plants	Long-term stem inventory data from tropical rain forest plots in Australia	34	1971	2013	-17.03808	145.561207	478	14938	Bradford MG, Murphy HT, Ford AJ, Hogan DL, Metcalfe DJ. Long‐term stem inventory data from tropical rain forest plots in Australia. Ecology. 2014;95(8):2362.
357	Terrestrial	Temperate	Mammals	Small Mammal Trapping Webs on the Central Plains Experimental Range	13	1994	2006	40.82889	-104.7582	10	1104	Stapp P. SGS-LTER Long-Term Monitoring Project: Small Mammals on Trapping Webs on the Central Plains Experimental Range, Nunn, Colorado, USA 1994 -2006, ARS Study Number 118. Environmental Data Initiative. 2013;Available at: http://dx.doi.org/10.6073/pasta/2e311b4e40fea38e573890f473807ba9:accessed 2017.
358	Terrestrial	Temperate	Birds	Neotropical Migratory Bird Communities in a Developing Pine Plantation	16	1977	1992	31.58333	-94.81666	14	140	Dickson JG, Conner RN, Williamson JH. Neotropical migratory bird communities in a developing pine plantation. Procedings Annu Conf SEAFWA. 1993;47:439–46.

359	Marine	Temperate	Fish	SBC LTER Reef Kelp Forest Community Dynamics Fish abundance	13	2000	2012	34.308906	-119.874156	61	3285	Reed DC. "SBC LTER: Reef: Kelp Forest Community Dynamics: Fish abundance". Santa Barbara Coastal LTER. 2014;Available at: doi:10.6073/pasta/e37ed29111b2fddffc08355252b8b8c7:accessed 2016.
361	Terrestrial	Temperate	Birds	A long-term bird population study in an Appalachian spruce forest	22	1962	1983	38.61	-79.83472	20	213	Hall GA. A long-term bird population study in an Appalachian spruce forest. Wilson Bull. 1984;228–40.
363	Terrestrial	Temperate	Birds	The 37-year dynamics of a subalpine bird community with special emphasis on the influence of environmental temperature and Epirrita autumnata cycles.	37	1963	1999	65.968055	16.31666	35	636	Enemar A, Sjöstrand B, Andersson G, von Proschwitz T. The 37-year dynamics of a subalpine passerine bird community, with special emphasis on the influence of environmental temperature and Epirrita autumnata cycles. Ornis Svecica. 2004;14:63–106.

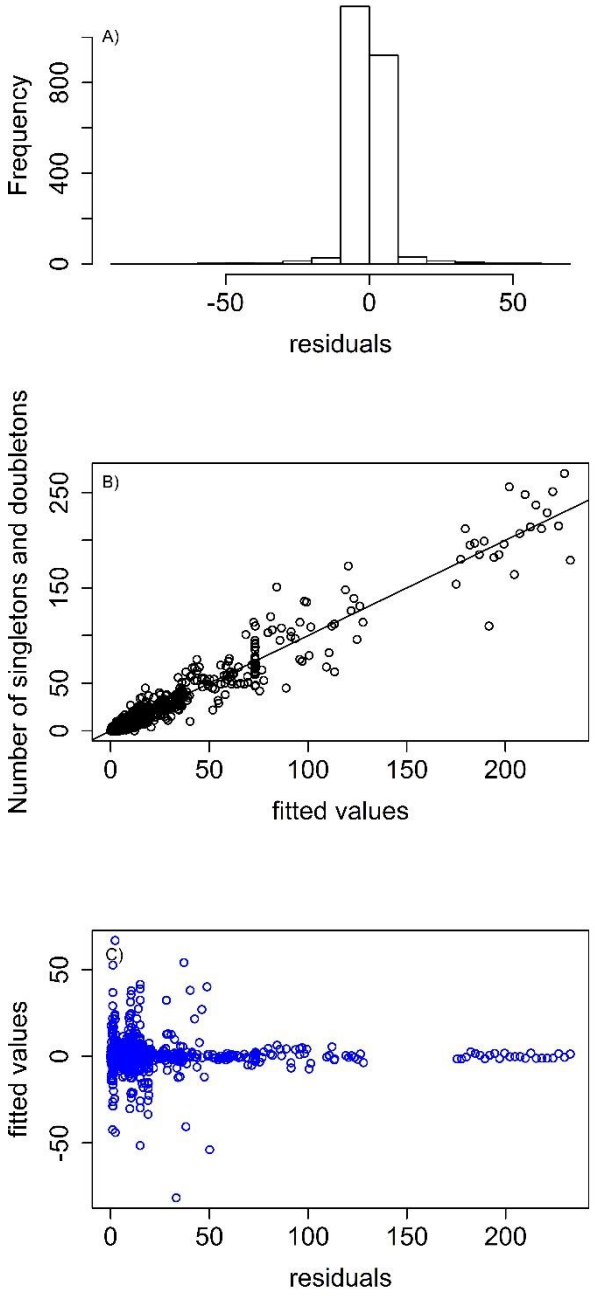
Appendix Chapter 5



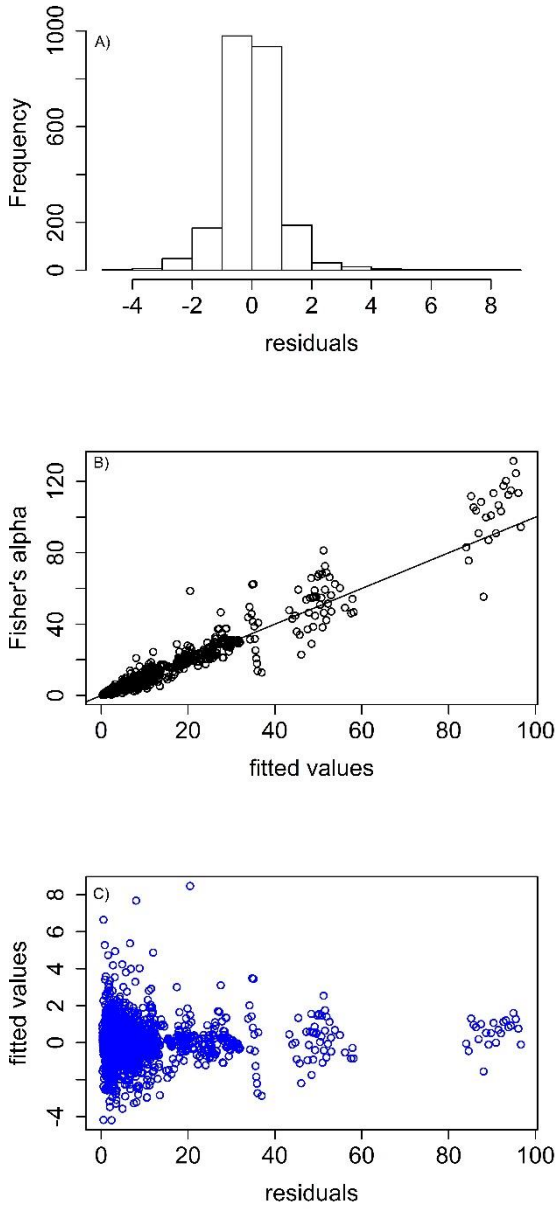
Appendix Figure 18. The model fit of the mixed effect model Equation 9a, regressing the number of singletons and doubletons within an assemblage each year against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



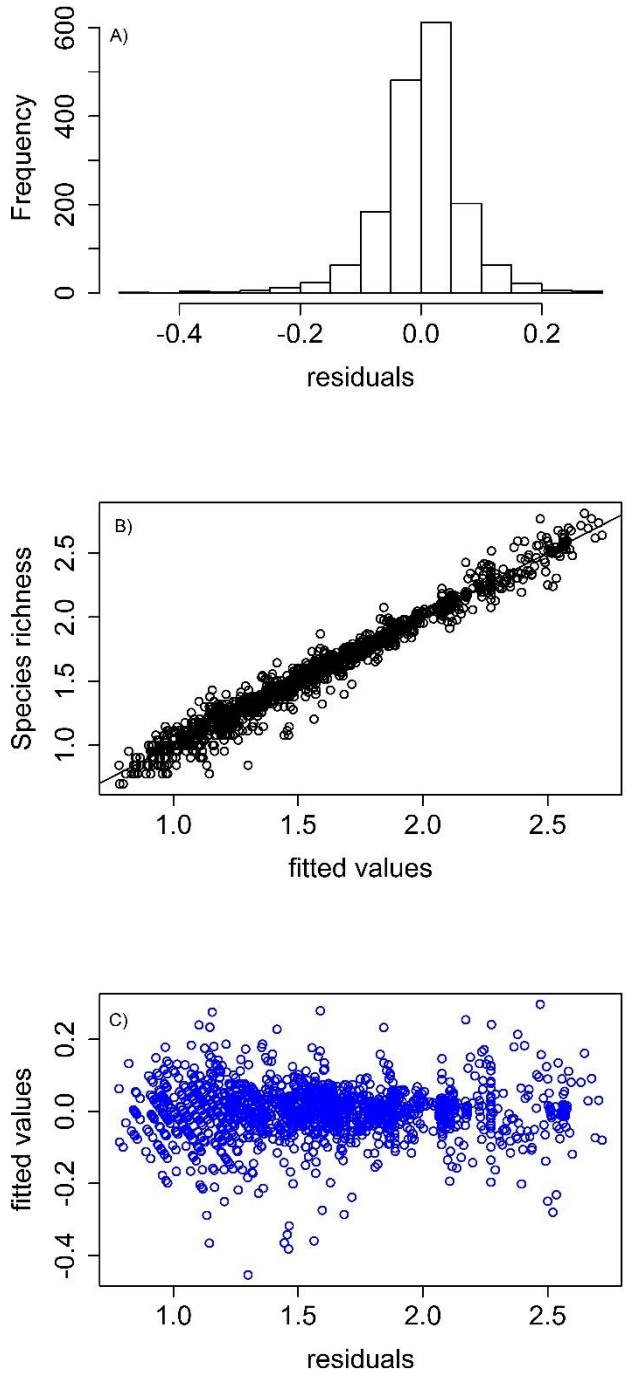
Appendix Figure 19. The model fit of the mixed effect model Equation 9b, regressing the number of singletons within an assemblage each year against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



Appendix Figure 20. The model fit of the mixed effect model Equation 11, regressing Fisher's alpha of an assemblage each year against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



Appendix Figure 21. The model fit of the mixed effect model Equation 12, regressing Fisher's alpha of an assemblage each year against mean-centred year. The model residuals are normally distributed (A) and the fitted values predict the actual empirical values well (B). There is, however, some evidence of heteroscedasticity (C). Because heteroscedasticity does not affect the direction of change of the model, and the model predicts data well, I decided to use this model structure despite the heteroscedasticity.



Appendix Figure 22. The model fit of the mixed effect model Equation 13, regressing the $\log_2$ species richness of an assemblage each year against mean-centred year. The model residuals are mostly normally distributed, although skewed to the right somewhat (A). The fitted values predict the actual empirical values well (B), and there is no evidence of heteroscedasticity (C).

Appendix Table 4. A list of all studies used in the Chapter 5 analysis.

These studies were sourced from the BioTIME database. This database is published as a data paper (Dornelas *et al*., 2018b) and can be access from http://biotime.st-andrews.ac.uk/home.php

Study ID	Realm	Climate	Taxa	Title	Number of years	Start year	End year	Central latitude	Central longitude	Number of Species	Total records	References
18	Terrestrial	Temperate	Terrestrial plants	Mapped quadrats in sagebrush steppe long-term data for analyzing demographic rates and plant-plant interactions	29	1923	1973	44.33	-112.33	98	8034	Zachmann L, Moffet C, Adler P. Mapped quadrats in sagebrush steppe: long-term data for analyzing demographic rates and plant–plant interactions. Ecology. 2010;91(11):3427-.
41	Terrestrial	Temperate	Birds	Time and space and the variation of species	10	1923	1940	39.5	-82.48	56	418	Preston FW. Time and space and the variation of species. Ecology. 1960;41(4):611-27.
42	Terrestrial	Temperate	Birds	Eastern Wood	30	1949	1979	51.2965	-0.38352	45	954	Gaston KJ, Blackburn TM. Pattern and process in macroecology. Oxford, England: Wiley-Blackwell; 2000. Beven G. Changes in breeding bird populations of an oak-wood on Bookham Common, Surrey, over twenty-seven years. London Naturalist. 1976;55:23-42. Gibbons DW, Reid JB, Chapman RA. The new atlas of breeding birds in Britain and Ireland: 1988-1991: T & AD Poyser London; 1993. Stone B, Sears J, Cranswick P, Gregory R, Gibbons D, Rehfisch M, *et al*. Population estimates of

												birds in Britain and in the United Kingdom. British Birds. 1997;90(1):1-22. Lack P. The atlas of wintering birds in Britain and Ireland: A&C Black; 2010. Standley P, Bucknell N, Swash A, Collins I. The Birds of Berkshire. Berkshire Atlas Group. Reading, UK. 1996. Williamson M, editor Are communities ever stable? Symposium of the British Ecological Society; 1987.
44	Terrestrial	Temperate	Terrestrial plants	Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3. 1962-Present	16	1962	1977	44.33	-122.33	158	25571	Halpern CB, Dyrness C. "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. 2010; Halpern CB, Lutz JA. Canopy closure exerts weak controls on understory dynamics: a 30‐year study of overstory–understory interactions. Ecological Monographs. 2013;83(2):221-37. Halpern CB, Lutz JA. "Canopy closure exerts weak controls on understory dynamics: a 30‐year study of overstory–

												understory interactions". 2013;Available at: Dryad DigitalRepository, doi:10.5061/dryad.1q88j:accessed 2013.
46	Terrestrial	Temperate	Birds	Skokholm Bird Observatory	47	1928	1979	51.698	-5.277	29	528	Williamson M. The land-bird community of Skokholm: ordination and turnover. Oikos. 1983:378-84.
47	Terrestrial	Temperate	Birds	Detection of Density-Dependent Effects in Annual Duck Censuses	26	1952	1977	50.84545	-107.446	13	392	Vickery WL, Nudds TD. Detection of Density‐Dependent Effects in Annual Duck Censuses. Ecology. 1984;65(1):96-104.
54	Terrestrial	Tropical	Terrestrial invertebrates	El Verde Grid invertebrate data (Big Grid Snail Captures 1991-2007)	24	1991	2014	18.1667	-65.5	19	21702	Willig MRB, C. P. . "El Verde Grid long-term invertebrate data: Luquillo Long Term Ecological Research Site Database: Data Set 107". 2016;Available at:http://luq.lternet.edu/data/luqmetadata107/7427 accessed 2016.
56	Terrestrial	Temperate	Mammals	Small Mammal Mark-Recapture Population Dynamics at Core Research Sites	20	1989	2008	34.2	-106.43	28	16657	Friggens M. "Sevilleta LTER Small Mammal Population Data", Albuquerque, NM: Sevilleta Long Term Ecological Research Site Database: SEV008. 2008;Available at: http://sev.lternet.edu/data/sev-8:accessed 2012.
57	Freshwater	Temperate	Fish	North Temperate Lakes LTER Fish Abundance	32	1981	2012	43.9928	-89.4946	76	10892	LTER N. "NTLFI02 North Temperate Lakes LTER: Fish Abundance 1981 - current". North Temperate Lakes Long Term Ecological Research program, NSF. Center for Limnology, University of Wisconsin-Madison.Available at:

												https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-fish-abundance-1981-current:accessed 2012.
58	Terrestrial	Tropical	Birds	Avian populations long-term monitoring dataset. San Juan. Puerto Rico Luquillo Long Term Ecological Research Site Database Grid points bird counts DBAS 23	18	1991	2008	18.19	-65.43	31	1171	Waide RB. Bird abundance - point counts. Long Term Ecological Research Network. 2010;Available at: http://dx.doi.org/10.6073/pasta/0d96957379936a038ebbbcc6135b2fab:accessed 2012. Waide RB. "Bird abundance - point counts. El Verde Field Station, Puerto Rico: Luquillo Long Term Ecological Research Site Database: Data Set 23". 2010;Available at: http:/luq.lternet.edu/data/luqmetadata23:accessed 2012.
59	Terrestrial	Temperate	Mammals	Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal. Arizona. USA	26	1977	2002	30.3226	-103.501	29	427	Ernest S, Valone TJ, Brown JH. Long‐term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology. 2009;90(6):1708-.
67	Terrestrial	Temperate	Birds	Animal Demography Unit - Coordinated Waterbird Counts (CWAC) (AfrOBIS)	24	1983	2006	-28.9545	24.95096	68	15448	CWAC. "Coordinated Waterbird Counts (CWAC) - AfrOBIS". .Available at: http://www.iobis.org/mapper/?dataset=603:accessed 2012.

81	Marine	Temperate	Mammals	CRRU Cetacean sighting in Scotland waters 1997-2010	14	1997	2010	57.76701	-2.643	9	1613	Robinson KP. "CRRU (Cetacean Research and Rescue Unit) Cetacean sightings in Scotland waters". 2010;Available at: http://www.emodnet-biology.eu/component/imis/?module=dataset&dasid=2819:accessed 2012. Robinson KP, Baumgartner N, Eisfeld SM, Clark NM, Culloch RM, Haskins GN, *et al*. The summer distribution and occurrence of cetaceans in the coastal waters of the outer southern Moray Firth in northeast Scotland (UK). Lutra. 2007;50(1):19.
97	Marine	Polar/Temperate	Marine invertebrates	Archives of the Arctic Seas Zooplankton (ARC)	22	1921	1973	72.73944	10.69445	402	15016	Markhaseva EL, Golikov AA, Agapova TA, Beig AA. Archives of the Arctic Seas Zooplankton. 1985;Available at: http://www.iobis.org/mapper/?dataset=4470:accessed 2012.
100	Marine	Temperate	Fish	Community level response to climate change The long-term study of the fish andcrustacean community of the Bristol Channel	31	1981	2011	51.14	-3.08	83	5199	Henderson PA. The long-term study of the fish and crustacean community of the Bristol Channel.Available at http://www.pisces-conservation.com/:accessed 2013. Henderson PA, Magurran AE. Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. Proceedings

												of the Royal Society B: Biological Sciences. 2014;281(1791). Henderson PA, Magurran AE. Data from: Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. Dryad Data Repository; 2014.
108	Marine	Global	Birds	Seabirds of the Southern and South Indian Ocean (Australian Antarctic Data Centre)	29	1977	2006	-27.1736	3.945813	123	116226	Woehler E. "Seabirds of the Southern and South Indian Ocean - Australian Antarctic Data Centre". Available at: http://www.iobis.org:accessed 2012.
112	Marine	Temperate/Tropical	Fish	NOAA Southeast Fishery Science Center (SEFSC) Commercial Pelagic Observer Program (POP) Data (SEFSC_POP)	22	1973	2005	24.98149	-51.3741	540	466437	NIWA. "South Western Pacific Regional OBIS Data Asteroid Subset", NIWA (National Institute of Water and Atmospheric Research - New Zealand) MBIS (Marine Biodata Information System) accessed through South Western Pacific OBIS.;Available at: http://www.iobis.org/mapper/?dataset=219:accessed 2012.
117	Marine	Temperate	Marine invertebrates	South Western Pacific Regional OBIS Data Asteroid Subset (South Western Pacific OBIS)	44	1956	2003	-39.3717	3.081897	156	2253	NODC. "South TX Outer Continental Shelf and MI, AL, and FL Outer Continental Shelf benthic organism sampling 1974-1978". US National Oceanographic Data Center, Silver Spring, Maryland, USA. 2011;Available at http://www.usgs.gov/obis-

												usa/data_search_and_access/participants.html:accessed 2012.
119	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	41	1970	2010	43.98743	-63.6697	231	121804	Clark D, Branton B. DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada. 2007.
125	Marine	Temperate	Fish	MARMAP Chevron Trap Survey 1990-2009 (OBIS-USA)	12	1988	2000	31.44165	-78.8489	101	15092	Reichert M. "MARMAP Chevron Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources U.S.A. 2009;Available at: http://www.usgs.gov/obis-usa/data_search_and_access/participants.html:accessed 2012.
163	Marine	Temperate	Benthos	North Pacific Groundfish Observer (North Pacific Research Board)	12	1993	2004	56.5	-168.15	355	419940	NPRB. "The Observer Program database", accessed through the OBIS-USA North Pacific Groundfish Observer (North Pacific Research Board). Available at: http://www.iobis.org:accessed 2012. .
166	Marine	Global	All	PIROP Northwest Atlantic 1965-1992 (SEAMAP)	25	1965	1992	36.07524	-70.9918	213	155600	Diamond A, Gaston A, Brown R. Converting PIROP Counts of Seabirds at Sea to Absolute Densities. Progress Notes No

												164. Canadian Wildlife Service, Ottawa. 1986. Huettmann F. An ecological GIS research application for the northern Atlantic-The PIROP database software, environmental data sets and the role of the internet. Riekert/Tochtermann. 1998. PIROP. "PIROP Northwest Atlantic 1965-1992 - OBIS SEAMAP".Available at: http://www.iobis.org/mapper/?dataset=2245:accessed 2012. Brown RG. Atlas of eastern Canadian seabirds. 1975. Halpin PN, Read AJ, Fujioka E, Best BD, Donnelly B, Hazen LJ, *et al*. OBIS-SEAMAP: The world data center for marine mammal, sea bird, and sea turtle distributions. Oceanography. 2009;22(2):104-15. Read A, Halpin P, Crowder L, Best B, Fujioka E. OBIS-SEAMAP: mapping marine mammals, birds and turtles. World Wide Web electronic publication http://seamap env duke edu Accessed. 2009;15.
169	Marine	Temperate	All	CalCOFI and NMFS Seabird and Marine Mammal	20	1987	2006	34.85846	-121.615	185	61730	Jahncke JR, C. "CalCOFI and NMFS Seabird and Marine Mammal Observation Data, 1987-2006". California

				Observation Data. 1987-2006 (SEAMAP)								Cooperative Oceanic Fisheries Investigations (CalCOFI) and National Marine Fisheries Service (NMFS) cruises, 1987-2006 - OBIS SEAMAP. 2006;Available at: http://www.iobis.org:accessed 2012. Rintoul C, Langabeer-Schlagenhauf B, Hyrenbach K, Morgan K, Sydeman W. Atlas of California Current marine birds and mammals: Version 1. Unpublished Report, PRBO Conservation Science, Petaluma, CA. 2006. Yen P, Sydeman W, Bograd S, Hyrenbach K. Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. Deep Sea Research Part II: Topical Studies in Oceanography. 2006;53(3):399-418. Yen PP, Sydeman WJ, Hyrenbach KD. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. Journal of Marine Systems. 2004;50(1):79-99.

172	Marine	Temperate	All	POPA cetacean. seabird. and sea turtle sightings in the Azores area 1998-2009 (OBIS SEAMAP)	12	1998	2009	35.00974	-24.2247	47	52291	POPA. "cetacean, seabird, and sea turtle sightings in the Azores area 1998-2009 - OBIS SEAMAP". .Available at: http://www.iobis.org/mapper/?dataset=4257:accessed 2012. Amorim P, Figueiredo M, Machete M, Morato T, Martins A, Serrão Santos R. Spatial variability of seabird distribution associated with environmental factors: a case study of marine Important Bird Areas in the Azores. ICES Journal of Marine Science. 2008;66(1):29-40. Machete M, Santos R, editors. Azores Fisheries Observer Program (POPA): a case study of the multidisciplinary use of observer data. Proceedings of the 5th International Fisheries Observer Conference; 2007. Morato T, Varkey DA, Damaso C, Machete M, Santos M, Prieto R, *et al*. Evidence of a seamount effect on aggregating visitors. Marine Ecology Progress Series. 2008;357:23-32.
180	Marine	Polar/Temperate	Fish	ECNASAP - East Coast North America Strategic Assessment (OBIS Canada)	26	1970	1995	37.77056	-50.7927	273	410802	ECNA. "East Coast North America Strategic Assessment Project, Groundfish Atlas for the East Coast of North America".Available at: http://www.iobis.org:accessed 2012.

182	Marine	Temperate	All	Snow crab research trawl survey database (Southern Gulf of St. Lawrence. Gulf region. Canada) from 1988 to 2010 (OBIS Canada)	22	1988	2009	47.48092	-62.7617	33	35005	Wade E. Snow crab research trawl survey database (Southern Gulf of St. Lawrence, Gulf region, Canada) from 1988 to 2010. OBIS Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada. 2011.
183	Marine	Temperate	Marine invertebrates	DFO Maritimes Research Vessel Trawl Surveys Invertebrate Observations (OBIS Canada)	13	1999	2011	43.77665	-63.7514	16	14906	Tremblay JM, Branton B. DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada. 2007.
190	Marine	Tropical	Fish	St. Croix. USVI Fish Assessment and Monitoring Data (2002 - Present) (NOAA-CCMA)	10	2001	2010	17.75697	-64.6043	247	28017	USVI. "St. Croix, USVI Fish Assessment and Monitoring Data (2002 - Present)", Silver Spring, MD Publisher: NOAAs Ocean Service, National Centers for Coastal Ocean Science (NCCOS). National Oceanic and Atmospheric Association (NOAA)-National Ocean Service (NOS)-National Centers for Coastal Ocean Science (NCCOS)-Center for Coastal Monitoring and Assessment (CCMA)-Biogeography Team. 2007;Available at: http://www.iobis.org/mapper/?dataset=1673:accessed 2012.
191	Marine	Temperate	Marine invertebrates	NEFSC Benthic Database (OBIS-USA)	28	1900	1975	39.12306	-66.6414	1614	51456	NEFSC. "Benthic Database (OBIS-USA)", Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Department of Commerce.

												2010;Available at: http://www.iobis.org/mapper/?dataset=1694:accessed 2012.
195	Terrestrial	Temperate	Birds	Breeding birds survey North America	30	1978	2007	40.80924	-96.1873	385	699449	USGS. Patuxent Wildlife Research Center "North American Breeding Bird Survey" ftp data set, version 2014.0.Available at: ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/:accessed 2013.
196	Marine	Temperate	Benthos	SOTEAG Rocky Shore Survey (Sullom Voe)	35	1976	2012	60.46645	-1.32288	252	91491	Moore JJ, Howson CM. "Survey of the rocky shores in the region of Sullom Voe, Shetland, A report to SOTEAG from Aquatic Survey & Monitoring Ltd", Cosheston, Pembrokeshire. 29 p.Available at: http://www.soteag.org.uk:accessed 2013.
200	Marine	Temperate	Marine invertebrates	NEFSC Benthic Database (OBIS-USA)	30	1956	1989	35.69171	-74.0908	2105	102143	DATRAS. "Fish trawl survey: Northern Irish Ground Fish Trawl Survey. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2764:accessed 2013.
206	Marine	Temperate	Fish	Northern Irish Ground Fish Trawl Survey	16	1993	2008	52.17598	-4.62847	108	13547	DATRAS. "Fish trawl survey: Northern Irish Ground Fish Trawl Survey. ICES Database of trawl surveys (DATRAS)." The International Council for the

												Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2764:accessed 2013.
208	Marine	Temperate	Fish	ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)	11	1997	2007	48.52178	-6.24898	189	24867	DATRAS. "Fish trawl survey: ICES French Southern Atlantic Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2759:accessed 2013.
209	Marine	Temperate	Fish	ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS) -UK	18	1990	2007	51.09476	0.085737	115	19711	DATRAS. "Fish trawl survey: ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2761:accessed 2013.
210	Marine	Temperate	Fish	ICES North Sea International Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)	47	1965	2011	56.46378	3.500367	254	296524	DATRAS. "Fish trawl survey: ICES North Sea International Bottom Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-

												biology.eu/data-catalog?%3Fmodule=dataset&dasid=2763:accessed 2013.
213	Marine	Temperate	Benthos	Northeast Fisheries Science Center Bottom Trawl Survey Data (OBIS-USA)	48	1948	2008	36.62513	-72.636	1023	439452	NMFS. "Northeast Fisheries Science Center Bottom Trawl Survey Data (OBIS-USA)." NOAA's National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center. Woods Hole, Massachusetts, USA. 2005;Available at: http://www.iobis.org/mapper/?dataset=1435:accessed 2013.
214	Terrestrial	Temperate	Terrestrial plants	Long-term growth mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest 1910 to present	88	1910	2010	45.34296	-122.799	39	37350	Harmon MF, J. "Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present." Long-Term Ecological Research. Forest Science Data Bank, Corvallis. 2012;Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TV010:accessed 2012.
215	Terrestrial	Temperate/Tropical	Birds	Hawk Migration Association of North America (HMANA)	57	1952	2008	38.40865	-99.5157	39	991769	HMANA. "Hawk Migration Association of North America (HMANA)".Available at: http://www.hmana.org/:accessed 2012.
217	Terrestrial	Temperate	Birds	Landbird Monitoring Program (UMT-LBMP)	14	1992	2006	46.82889	-109.982	268	336516	USFS. "Landbird Monitoring Program (UMT-LBMP)." US Forest Service.Available at: http://www.avianknowledge.net/:accessed 2012.

219	Terrestrial	Temperate	Amphibians	Marsh Monitoring Program - Amphibian Surveys	17	1995	2011	44.90047	-84.7768	14	41914	NatureCounts. Bird Studies Canada "Marsh Monitoring Program." NatureCounts, a node of the Avian Knowledge Network. 2012;Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
220	Terrestrial	Temperate	Birds	Marsh Monitoring Program - Bird Surveys	17	1995	2011	46.88548	-80.0332	243	144779	NatureCounts. Bird Studies Canada "Marsh Monitoring Program." NatureCounts, a node of the Avian Knowledge Network. 2012;Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
221	Terrestrial	Temperate	Terrestrial plants	Vegetation Plots of the Bonanza Creek LTER Control Plots Species Count (1975 - 2004)	26	1975	2008	64.84423	-148.052	52	1157	Viereck LA, Van Cleve K, Chapin FS, Ruess RW, Hollingsworth TN. Vegetation Plots of the Bonanza Creek LTER Control Plots: Species Count (1975 - 2004). Environmental Data Initiative. 2005;Available at: http://dx.doi.org/10.6073/pasta/8dd0e1ac48e2f82b51adabfbd3c62ae2:accessed 2012.
225	Terrestrial	Temperate	Birds	Point count bird censusing long-term monitoring of bird distrubution and diversity in central Arizona-Phoenix period 2000 to 2011	12	2000	2011	33.43	-111.93	278	48841	Shochat E, Katti M, Warren P. “Point count bird censusing: long-term monitoring of bird distribution and diversity in central Arizona-Phoenix: period 2000 to 2011”. Central Arizona-Phoenix Long-Term Ecological Research. Global Institute for Sustainability, Arizona State University. 2004;Available at:

												https://caplter.asu.edu/data/data-catalog/?id=46:accessed 2012.
229	Freshwater	Temperate	Fish	Upper Little Tennessee River Biomonitoring Program Database - LTWA Biomonitoring Database	26	1988	2013	35.13816	-83.3855	69	11184	McLarney WO, Meador J, Chamblee J. "Upper Little Tennessee River Biomonitoring Program Database." Coweeta Long Term Ecological Research Program. 2010;Available at: https://coweeta.uga.edu/dbpublic/dataset_details.asp?accession=4045:accessed 2012.
232	Marine	Polar/Temperate	Fish	Pelagic Fish Observations 1968-1999	25	1968	1999	-56.8147	93.88436	185	6446	Williams D. "Pelagic Fish Observations 1968-1999." Australian Antarctic Data Centre.Available at: http://www.gbif.org/dataset/85b0a82a-f762-11e1-a439-00145eb45e9a:accessed 2012.
236	Freshwater	Temperate	Fish	Fish population on selected watersheds at Konza Prairie - CFP012 - Konza fish population	12	1995	2006	39.0931	-96.5586	19	1169	Gido KB. "Fish population on selected watersheds at Konza Prairie - CFP01." Konza Prairie LTER Program.Available at: http://www.konza.ksu.edu/KNZ/pages/data/Knzdsdetail.aspx?datasetCode=CFP01:accessed 2012.
240	Terrestrial	Temperate	Terrestrial plants	Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta National Wildlife Refuge New	13	2003	2015	34.35	-106.88	167	15561	Muldavin E. "Pinon-Juniper (Core Site) Quadrat Data for the Net Primary Production Study at the Sevilleta National Wildlife Refuge, New Mexico (2003-Present)." Sevilleta Long Term Ecological Research Program.;Available at: http://sev.lternet.edu/node/1718:accessed 2013.

				Mexico (2003-present)								
243	Terrestrial	Temperate	Terrestrial plants	Long-term N-fertilized vegetation plots on Hog Island Virginia Coastal Barrier Islands 1992 to 2014	22	1992	2014	37.44663	-75.6675	51	8508	Day F. "Long-term N-fertilized vegetation plots on Hog Island, Virginia Coastal Barrier Islands, 1992-2014." Virginia Coast Reserve Long-Term Ecological Research Project. 2010;Available at: http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.106:accessed 2013. Day FP, Conn C, Crawford E, Stevenson M. Long-term effects of nitrogen fertilization on plant community structure on a coastal barrier island dune chronosequence. Journal of Coastal Research. 2004:722-30.
244	Marine	Temperate	Birds	British Columbia Coastal Waterbirds Survey	14	1999	2012	50.55543	-126.284	243	219126	NatureCounts. Bird Studies Canada "BC Coastal Waterbird Survey (2004)." NatureCounts, a node of the Avian Knowledge Network. 2012;Available at: http://www.birdscanada.org/birdmon/:accessed 2012.
246	Marine	Temperate	Fish	Long-term monitoring dataset of fish assemblages impinged at nuclear power	15	2000	2014	25.24431	121.6243	335	3722	Chen H, Liao Y-C, Chen C-Y, Tsai J-I, Chen L-S, Shao K-T. Long-term monitoring dataset of fish assemblages impinged at nuclear power plants in northern

				plants in northern Taiwan								Taiwan. Scientific data. 2015;2:150071.
249	Terrestrial	Temperate	Terrestrial invertebrates	Resource specialists lead local insect community turnover associated with temperature - analysis of an 18-year full-seasonal record of moths and beetles	24	1992	2015	55.70251	12.55896	1427	31787	Thomsen PF, Jørgensen PS, Bruun HH, Pedersen J, Riis-Nielsen T, Jonko K, *et al*. Resource specialists lead local insect community turnover associated with temperature – analysis of an 18-year full-seasonal record of moths and beetles. Journal of Animal Ecology. 2016;85(1):251-61.
252	Marine	Temperate	Fish	MARMAP Blackfish Trap Survey 1990-2009	13	1977	1989	32.45388	-78.9682	48	4692	Reichert M. "MARMAP Blackfish Trap Survey 1990-2009". SCDNR/NOAA MARMAP Program. SCDNR MARMAP Aggregate Data Surveys. The Marine Resources Monitoring. Assessment. and Prediction (MARMAP) Program. Marine Resources Research Institute. South Carolina Department of Natural Resources USA. 2010;Available at: http://www.usgs.gov/obis-usa/:accessed 2013.
253	Freshwater	Temperate	Freshwater invertebrates	North Temperate Lakes LTER Zooplankton - Trout Lake Area 1982 - current	29	1986	2014	46.02139	-89.6529	133	30750	LTER N. "North Temperate Lakes LTER: Zooplankton - Trout Lake Area 1982 - current." NorthTemperate Lakes Long Term Ecological Research Program, Center for Limnology, University of Wisconsin-Madison.Available at: https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-

												lter-zooplankton-trout-lake-area-1982-current:accessed 2013.
256	Marine	Temperate	Fish	ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS) - The Netherlands	24	1987	2010	56.34138	2.672616	120	37250	DATRAS. "Fish trawl survey: ICES Beam Trawl Survey for commercial fish species. ICES Database of trawl surveys (DATRAS)." The International Council for the Exploration of the Sea, Copenhagen. 2010;Available at: http://www.emodnet-biology.eu/data-catalog?%3Fmodule=dataset&dasid=2761:accessed 2013.
271	Marine	Temperate	Fish	Santa Barbara Coastal LTER	15	2000	2014	34.30565	-119.875	62	6287	Reed DC. “SBC LTER: Reef: Kelp forest community dynamics: Abundance and size of giant kelp (Macrocystis pyrifera), ongoing since 2000”. Santa Barbara Coastal LTER. 2014a;Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-sbc.18 doi:10.6073/pasta/d90872297e30026b263a119d4f5bca9f:accessed 2016.
272	Marine	Temperate	Marine invertebrates	Santa Barbara Coastal LTER	15	2000	2014	34.30554	-119.876	36	5363	Reed DC. “SBC LTER: Reef: Kelp forest community dynamics: Fish abundance”. Santa Barbara Coastal LTER. 2014b;Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-sbc.17 doi:10.6073/pasta/e37ed29111b2fddffc08355252b8b8c7:accessed 2016.

273	Marine	Temperate	Marine invertebrates	Santa Barbara Coastal LTER	15	2000	2014	34.30554	-119.876	27	15498	Reed DC. "SBC LTER: Reef: Kelp forest community dynamics: Invertebrate and algal density". Santa Barbara Coastal LTER. . 2014c;Available at: http://sbc.lternet.edu/cgi-bin/showDataset.cgi?docid=knb-lter-sbc.19 doi:10.6073/pasta/cd4cf864efecd69891dfe1d73b9ac9c3:accessed 2016.
288	Marine	Temperate	Fish	DFO Maritimes Research Vessel Trawl Surveys Fish Observations (OBIS Canada)	34	1970	2006	43.97739	-63.682	195	19074	Clark D, Branton B. DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada. 2007.
297	Marine	Tropical	Marine invertebrates	MCR LTERCoral Reef Long-term Population and Community Dynamics Other Benthic Invertebrates. ongoing since 2005	11	2005	2015	-17.5246	-149.837	13	2734	Carpenter R. "MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Other Benthic Invertebrates, ongoing since 2005". Moorea Coral Reef LTER, knb-lter-mcr.7.28. 2015;Available at: doi:10.6073/pasta/8e7b3a0c7a8bf315739921861cc79d10:accessed 2016.
300	Terrestrial	Temperate	Terrestrial invertebrates	Insect Populations via Sticky Traps at KBS-LTER (Kellogg Biological Station. MI)	25	1989	2013	42.40885	-85.3832	21	47798	Landis D, Gage S. Insect Populations via Sticky Traps at KBS-LTER. 2014;Available at: http://lter.kbs.msu.edu/datatables/67:accessed 2016.

301	Terrestrial	Temperate	Terrestrial invertebrates	Konza LTER grasshopper monitoring. Konza Prairie LTER. KS	25	1982	2013	39.106	-96.611	51	10470	Joern A. CGR02 Sweep Sampling of Grasshoppers on Konza Prairie LTER watersheds (1982-present). Environmental Data Initiative. 2016;Available at: http://dx.doi.org/10.6073/pasta/7060b2c244229a37e3bfc8c18f14ad02:accessed 2016. Jonas JL, Joern A. Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: a long-term study. Oecologia. 2007;153(3):699-711.
308	Terrestrial	Temperate	Mammals	Powdermill Nature Reserve monitored small mammal populations from 1979-1999.	21	1979	1999	40.17074	-79.2602	14	35398	Merritt J. Long Term Mammal Data from Powdermill Biological Station 1979-1999. Environmental Data Initiative. 1999;Available at: http://dx.doi.org/10.6073/pasta/83c888854e239a79597999895bb61cfe:accessed 2016.
309	Terrestrial	Temperate	Terrestrial invertebrates	Monitoring the Abundance of Butterflies 1976-1985	10	1976	1985	53.13218	-2.17768	44	5694	Pollard E, Hall ML, Bibby TJ. Monitoring the Abundance of Butterflies 1976-1985. Research & survey in nature conservation. 1986;Available at: http://jncc.defra.gov.uk/page-2614:accessed 2016.
311	Terrestrial	Temperate	Mammals	Seasonal summary of numbers of small mammals on 14 LTER traplines in	33	1981	2013	39.08333	-96.5833	15	2458	Kaufman DW. Seasonal summary of numbers of small mammals on 14 LTER traplines in prairie habitats at Konza Prairie. Konza Prairie Long-Term Ecological Research. .Available at:

				prairie habitats at Konza Prairie								http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza:accessed 2016.
313	Terrestrial	Temperate	Terrestrial invertebrates	Successional Dynamics on a Resampled Chronosequence Core Old Field Grasshopper Sampling	18	1989	2006	45.4	-93.2	61	7958	Knops J, Tilman D. Successional Dynamics on a Resampled Chronosequence - Experiment 014. Cedar Creek Ecosystem Science Reserve. .Available at http://www.cedarcreek.umn.edu/research/data/dataset?ghe014:accessed 2016.
316	Terrestrial	Temperate	Reptiles	Lizard pitfall trap data (LTER-II LTER-III)	18	1989	2006	32.62	-106.74	21	2650	Lightfoot D. “Lizard pitfall trap data (LTER-II, LTER-III)”. Jornada Basin LTER. 2013;Available at: http://jornada.nmsu.edu/lter/dataset/49821/view:accessed 2016.
318	Terrestrial	Temperate	All	Karoo National Park Census Data	13	1994	2009	-32.2333	22.28333	25	229	SANParks. "Karoo National Park Census Data. 1994 - 2009". 2011;Available at: http://datadryad.org/handle/10255/dryad.13079?show=full:accessed 2016.
319	Terrestrial	Temperate	All	Effects of rangeland management on community dynamics of herpetofauna to the tallgrass prairie	14	1989	2003	37.25	-96.7167	35	232	Wilgers DJ, Horne EA, Sandercock BK, Volkmann AW. Effects of rangeland management on community dynamics of the herpetofauna of the tallgrass prairie. Herpetologica. 2006;62(4):378-88.

321	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study. Jornada LTER. SMES rodent trapping data	13	1995	2007	32.55034	-106.812	19	12787	Lightfoot D, Schooley RL. "SMES rodent trapping data, Small Mammal Exclosure Study". Jornada LTER.Available at: http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/data_files/JornadaStudy_086_smes_rodent_trapping_data_0.csv:accessed 2016.
327	Terrestrial	Temperate	Mammals	Fray Jorge Small Mammals 1989-2005	17	1989	2005	-30.6	-71.7	12	256469	Kelt D, Meserve P, Gutiérrez J, Milstead WB, Previtali M. Long‐term monitoring of mammals in the face of biotic and abiotic influences at a semiarid site in north‐central Chile. Ecology. 2013;94(4):977-.
328	Freshwater	Temperate	Amphibians	The Rainbow Bay Long-term Study	30	1979	2008	32.26	-81.63	10	301	Scott D, Metts B, Lance S. "The Rainbow Bay Long-term Study".Available at: http://srelherp.uga.edu/projects/rbay.htm:accessed 2016.
332	Freshwater	Temperate	Fish	Stream Fish Assemblage stability in a southern Appalachian stream (Coweeta Hydro Lab 1984 - 1995)	12	1984	1995	35.0589	-83.4319	14	590	Grossman GD. "Stream fish assemblage stability in a southern Appalachian stream at the Coweeta Hydrologic Laboratory from 1984 to 1995". Coweeta Long Term Ecological Research Program. 2007;Available at: http://dx.doi.org/10.6073/pasta/f0baf5f59c89f670e04f537f5cc05290:accessed 2016.

336	Terrestrial	Temperate	Terrestrial plants	Long term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal Arizona	14	1989	2002	31.93889	-109.08	100	35978	Ernest S, Valone TJ, Brown JH. Long‐term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology. 2009;90(6):1708-.
339	Terrestrial	Temperate	Birds	Species trends turnover and composition of a woodland bird community in southern Sweden during a period of 57 years.	57	1953	2009	55.71667	13.33333	39	1210	Svensson S, Thorner A, Nyholm N. Species trends, turnover and composition of a woodland bird community in southern Sweden during a period of fifty-seven years. Ornis Svecica. 2010;20(1):31-44.
340	Terrestrial	Temperate	Terrestrial plants	Small Mammal Exclosure Study (SMES) Vegetation Data from the Chihuahuan Desert	15	1995	2009	34.296	-106.927	93	1608	Lightfoot D. "Small Mammal Exclosure Study (SMES) Vegetation Data from the Chihuahuan Desert Grassland and Shrubland at the Sevilleta National Wildlife Refuge, New Mexico (2006-2009)". Long Term Ecological Research Network. 2011;Available at: http://dx.doi.org/10.6073/pasta/d80d5e2196cd11ef79df23ebe5a77c19:accessed 2016.
348	Terrestrial	Temperate/Tropical	Mammals	Bats (Mammalia Chiroptera) in restinga in the municipality of Jaguaruna south of Santa Catarina Brazil.	10	2006	2016	-28.6089	-48.9813	13	177	Carvalho F, Zocche JJ, Mendonça RÁ. Morcegos (Mammalia, Chiroptera) em restinga no município de Jaguaruna, sul de Santa Catarina, Brasil. Biotemas. 2009;22(3):193-201.
356	Terrestrial	Tropical	Terrestrial plants	Long-term stem inventory data from tropical	34	1971	2013	-17.0381	145.5612	478	14938	Bradford MG, Murphy HT, Ford AJ, Hogan DL, Metcalfe DJ. Long‐term stem inventory data

				rain forest plots in Australia								from tropical rain forest plots in Australia. Ecology. 2014;95(8):2362-.
357	Terrestrial	Temperate	Mammals	Small Mammal Trapping Webs on the Central Plains Experimental Range	13	1994	2006	40.82889	-104.758	10	1104	Stapp P. SGS-LTER Long-Term Monitoring Project: Small Mammals on Trapping Webs on the Central Plains Experimental Range, Nunn, Colorado, USA 1994 -2006, ARS Study Number 118. Environmental Data Initiative. 2013;Available at: http://dx.doi.org/10.6073/pasta/2e311b4e40fea38e573890f473807ba9:accessed 2017.
359	Marine	Temperate	Fish	SBC LTER Reef Kelp Forest Community Dynamics Fish abundance	13	2000	2012	34.30891	-119.874	61	3285	Reed DC. "SBC LTER: Reef: Kelp Forest Community Dynamics: Fish abundance". Santa Barbara Coastal LTER. 2014;Available at: doi:10.6073/pasta/e37ed29111b2fddffc08355252b8b8c7:accessed 2016.
361	Terrestrial	Temperate	Birds	A long-term bird population study in an Appalachian spruce forest	22	1962	1983	38.61	-79.8347	20	213	Hall GA. A long-term bird population study in an Appalachian spruce forest. The Wilson Bulletin. 1984:228-40.
366	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study (SMES)	25	1989	2013	34.35	-106.88	24	3389	Lightfoot D. "Small Mammal Exclosure Study (SMES)". Sevilleta Long Term Ecological Research Program.Available at: http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0:accessed 2016.
374	Marine	Temperate	Birds	Monitoring site 1000 Shorebird Survey	11	2004	2014	35.96125	136.0461	70	38674	Monitoring Site 1000 Project, Biodiversity Center, Japan MoEo. "Monitoring site 1000 Shorebird

												Survey" 2013;(ShorebirdsDatapackage2012.zip, downloaded from http://www.biodic.go.jp/moni1000/findings/data/index.html):Accessed 2016.
375	Terrestrial	Temperate	Terrestrial invertebrates	Surface of the earth wandering beetles survey data	11	2004	2014	36.24489	136.9066	424	19937	Monitoring Site 1000 Project, Biodiversity Center, Japan MoEo. "Monitoring site 1000 Forest and grassland research - Surface wandering beetles survey data". 2014;(GBDataPackage2014ver1.zip, downloaded from http://www.biodic.go.jp/moni1000/findings/data/index.html):Accessed 2016.
378	Marine	Temperate	Marine invertebrates	Calafuria Mid-shore Intertidal Dataset (1991-2014)	16	1991	2006	43.46937	10.33596	42	1239	Benedetti-Cecchi L. "Calafuria Mid-shore Intertidal Dataset (1991-2014)". Department of Biology, University of Pisa.Accessed 2016.
379	Marine	Temperate	Marine invertebrates	Calafuria Low-shore Intertidal Dataset (1991-2014)	22	1991	2014	43.46937	10.33596	61	1153	Benedetti-Cecchi L. "Calafuria Mid-shore Intertidal Dataset (1991-2014)". Department of Biology, University of Pisa.Accessed 2016.
380	Terrestrial	Temperate	Terrestrial invertebrates	Monitoring butterfly numbers	10	1978	1987	50.8463	0.0552	23	217	Pollard E. Monitoring butterfly numbers. In: F. B.Goldsmith (ed). Monitoring for Conservation and Ecology Chapman and Hall. 1991. NERC. "The Global Population Dynamics Database Version 2". Centre for Population Biology,

												Imperial College. 2010;Available at: http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html:accessed 2016.
382	Terrestrial	Temperate	Mammals	Small Mammals and Vegetation Changes After Fire in a Mixed Conifer-Hardwood Forest	13	1955	1967	47.83333	-91.8333	7	214	NERC. "The Global Population Dynamics Database Version 2". Centre for Population Biology, Imperial College. 2010;Available at: http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html:accessed 2016. Krefting LW, Ahlgren CE. Small Mammals and Vegetation Changes After Fire in a Mixed Conifer - Hardwood Forest. Ecology. 1974;55(6):1391-8.
419	Marine	Temperate	Birds	Data collected aboard cruises off the coast of the Western Antarctic Penninsula	19	1993	2011	-64.77	-64.05	54	3050	Fraser W. "At-sea seabird censuses. Data on the species encountered (including marine mammals), their abundance, distribution and behavior. Data collected aboard cruises off the coast of the Western Antarctic Peninsula, 1993 - present". Palmer Station Antarctica LTER. 2014;Available at: http://dx.doi.org/10.6073/pasta/e3871e749fa737dd94d5a269ac90e8ce:accessed 2016.
420	Terrestrial	Polar/Temperate	Birds	Species composition and population fluctuations of alpine bird communities during 38 years	38	1964	2001	67.077	17.435	47	1010	Svensson S. Species composition and population fluctuations of alpine bird communities during 38 years in the Scandinavian mountain range. Ornis Svecica. 2006;16(4):183-210.

				in the Scandinavian mountain range								
428	Marine	Temperate	All	Long term monitoring of fish abundances from coastal SKagerrak	97	1919	2015	58.95856	9.768152	59	101221	Olsen EM, Carlson SM, Gjøsæter J, Stenseth NC. Nine decades of decreasing phenotypic variability in Atlantic cod. Ecology Letters. 2009;12(7):622-31. Rogers LA, Stige LC, Olsen EM, Knutsen H, Chan K-S, Stenseth NC. Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. Proceedings of the National Academy of Sciences. 2011;108(5):1961-6. Stenseth NC, Bjørnstadf ON, Falck W, Fromentin JM, Gjøsieter J, Gray JS. Dynamics of coastal cod populations: intra- and intercohort density dependence and stochastic processes. Proceedings of the Royal Society of London Series B: Biological Sciences. 1999;266(1429):1645-54. Barceló C, Ciannelli L, Olsen EM, Johannessen T, Knutsen H. Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Global Change Biology. 2016;22(3):1155-67.

430	Freshwater	Temperate	Fish	The New Zealand Freshwater Fish Database - Electric fishing - Backpack	32	1985	2016	-40.9428	172.4993	57	22054	NIWA. "The New Zealand Freshwater Fish Database".Available at: https://www.niwa.co.nz/our-services/online-services/freshwater-fish-database:accessed 2016.
431	Freshwater	Temperate	Fish	The New Zealand Freshwater Fish Database - Traps- Gee Minnow traps	33	1984	2016	-40.6336	172.4499	44	3804	NIWA. "The New Zealand Freshwater Fish Database".Available at: https://www.niwa.co.nz/our-services/online-services/freshwater-fish-database:accessed 2016.
432	Freshwater	Temperate	Fish	The New Zealand Freshwater Fish Database - Observation (Spotlighting visual)	19	1998	2016	-40.4926	172.7156	36	3520	NIWA. "The New Zealand Freshwater Fish Database".Available at: https://www.niwa.co.nz/our-services/online-services/freshwater-fish-database:accessed 2016.
441	Terrestrial	Temperate	Birds	Long-term dynamics of bird populations in birch forests of Ilmen Nature Reserve during the breeding period individuals / km2	13	1985	1997	54.50408	60.294	61	384	Zakharov VD. Biodiversity of bird population of terrestrial habitats in Southern Ural. Miass: IGZ. Ural Branch of Russian Academy of Sciences. 1998:158 p.
466	Marine	Temperate	Fish	Trawl Survey Data from Rockall Scotland (1986 - 2008)	23	1986	2008	56.99054	-9.07255	94	27592	Neat F, Campbell N. Demersal fish diversity of the isolated Rockall plateau compared with the adjacent west coast shelf of Scotland. Biological Journal of

												the Linnean Society. 2011;104(1):138-47.
471	Terrestrial	Temperate	Terrestrial plants	Prescribed Burn Effect on Chihuahuan Desert Grasses and Shrubs at the Sevilleta National Wildlife Refuge	10	2004	2013	34.35	-106.88	162	37979	Muldavin E, Collins SL. Prescribed Burn Effect on Chihuahuan Desert Grasses and Shrubs at the Sevilleta National Wildlife Refuge, New Mexico: Species Composition Study 2004 to present. Sevilleta LTER. 2003;Available at: http://sev.lternet.edu/data/sev-166:accessed 2016.
473	Terrestrial	Temperate	Terrestrial plants	Fourteen years of mapped permanent quadrats in a northern mixed prairie	14	1932	1945	46.31667	-105.8	95	2350	Anderson J, Vermeire L, Adler PB. Fourteen years of mapped, permanent quadrats in a northern mixed prairie, USA. Ecology. 2011;92(8):1703-.
475	Terrestrial	Temperate	Birds	Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest	12	1960	1972	63.41667	10.5	34	327	Hogstad O, editor Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest. A 12-year study. Annales Zoologici Fennici; 1993: JSTOR.
477	Marine	Temperate	Marine invertebrates	Epifaunal invertebrate survey from Goodwin Islands York River Estuary Chesapeake Bay	15	1998	2012	37.222	-76.392	41	5914	Douglass JG, France KE, Richardson JP, Duffy JE. Seasonal and interannual change in a Chesapeake Bay eelgrass community: Insights into biotic and abiotic control of community structure. Limnology and Oceanography. 2010;55(4):1499-520. Lefcheck JS. The use of functional traits to elucidate the causes and consequences of

												biological diversity. The College of William & Mary, PhD thesis. 2015;Available at: http://gradworks.umi.com/36/62/3662989.html:accessed 2016.
478	Freshwater	Temperate	Freshwater invertebrates	Long term study of the stream ecosystems in the Breitenbach	37	1969	2005	50.66972	9.628889	90	1537	Wagner R, Marxsen J, Zwick P, Cox EJ. Central European Stream Ecosystems: The Long Term Study of the Breitenbach: John Wiley & Sons; 2011

Publications arising from this thesis

Quantifying regional biodiversity in the tropics: a case study of freshwater fish in Trinidad and Tobago

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Abstract

Extinction rates are predicted to accelerate during the Anthropocene. Quantifying and mitigating these extinctions demands robust data on distributions of species and the diversity of taxa in regional biotas. However, many assemblages, particularly those in the tropics, are poorly characterized. Targeted surveys and historical museum collections are increasingly being used to meet the urgent need for accurate information, but the extent to which these contrasting data sources support meaningful inferences about biodiversity change in regional assemblages remains unclear. Here we seek to elucidate uncertainty surrounding regional biodiversity estimates by evaluating the performance of these alternative methods in estimating the species richness and assemblage composition of the freshwater fish of Trinidad and Tobago.

We compared estimates of regional species richness derived from two freshwater fish datasets: a targeted two year survey of Trinidad and Tobago rivers and historical museum collection records submitted to The University of the West Indies Zoology Museum. Richness was estimated using rarefaction and extrapolation, and assemblage composition was benchmarked against a recent literature review. Both datasets provided similar estimates of regional freshwater fish species richness (50 and 46 species, respectively), with a large overlap (85%) in species identities. Regional species richness estimates based on survey and museum data are thus comparable, and consistent in the species they include. Our results suggest that museum collection data are a viable option for setting reliable baselines in many tropical systems, thereby widening options for meaningful monitoring and evaluation of temporal trends.

Assemblage composition; museum collections; species richness; neotropics; rarefaction; extrapolation

Introduction

Although there is general agreement that we have entered the Anthropocene, an era likely to be characterised by mass extinctions (Barnosky *et al*., 2011; Dirzo & Raven, 2003), there are substantial gaps in our understanding of biodiversity change, particularly at regional scales (McGill, Dornelas, Gotelli, & Magurran, 2015), and considerable uncertainty about extinction rates (Ceballos *et al*., 2015). Many assemblages, notably those in the tropics, are poorly characterised (Coddington, Agnarsson, Miller, Kunter, & Hormiga, 2009; Collen, Ram, Zamin, & McRae, 2008). Even in well-

sampled areas many species are very rare, and are recorded in surveys only as singletons or "uniques" (Longino, Coddington, & Colwell, 2002). The presence of uniques in species accumulation curves is a strong indicator that unseen species are yet to be detected (Chao, 1984). One solution is to use statistical estimation approaches to deduce the number of unseen species in survey data (i.e. Chao & Jost, 2012; Gotelli & Colwell, 2001; Gotelli & Colwell, 2011).

Historical natural history museum records and herbarium collections are potential sources of data for biodiversity estimation, and are increasingly used to address ecological and conservation questions (Pyke & Ehrlich, 2010; Reznick, Baxter, & Endler, 1994). There are, though, concerns about possible biases in this type of data, particularly in terms of spatial representation and sampling bias (Fattorini, 2013; Guralnick & Van Cleve, 2005; Newbold, 2010).

The extent to which these different data sources provide meaningful inferences about biodiversity change in regional assemblages remains unclear. Survey data, on the one hand, may underestimate species richness to a greater extent than museum records because sampling is generally targeted at specific areas or habitats, or depends on methods which may incompletely record certain taxa (Guralnick & Van Cleve, 2005). For example, species that are known or suspected to be abundant in the sample area but are not easily recorded using the sampling methodology (Longino *et al*., 2002). On the other hand, while museums typically seek to maximise the range of specimens in the collection, they rarely set out to enumerate the species that co-occur in functioning ecosystems. Comprehensive species lists are accumulated over time, and often include transient taxa and misidentifications, so such lists are not necessarily an informative guide to the species actually present in an assemblage during a defined time period (Phillip *et al*., 2013).

Previous assessments of the relative utility of biodiversity quantifications from survey data and museum collections have focused on species richness rather than species identities (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). However, biodiversity change can be substantially decoupled from species richness change when there is extensive turnover within assemblages (Dornelas *et al*., 2014; Hillebrand *et al*., 2017; Vellend *et al*., 2013, 2017). Accurate assessment of turnover (beta diversity), both spatial and temporal, is becoming increasingly important to understanding biodiversity change (Dornelas *et al*., 2014; McGill *et al*., 2015). There is consequently a need to recognize uncertainties and biases not only of species richness estimates, but also of species identities recorded within these contrasting datatypes. For example, previous research suggests that while museum records may provide useful estimates of richness, species identities may be biased towards rare species (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). This is of particular concern if species lists derived from one sampling method will be used as baselines for further assessments using data collected with other methods.

Here we ask how conclusions about the biodiversity of freshwater fish in Trinidad and Tobago differ when based on a targeted survey versus a museum collection. First, we evaluate the performance of these alternative data sources when estimating the species richness of the freshwater fish fauna, and benchmark our results against a recent literature review. Secondly, we analyse the identities of species recorded by both methods to assess which species are absent, and to pinpoint possible biases in types of species detected.

Our initial expectations regarding biases in the datasets are as follows:

1. The museum data will contain more transient species than the survey data because the longer period of time covered by the museum data increases the chance of finding a species that subsequently becomes locally extinct.

2. There will be more species with specialized habitat requirements or narrow spatial distributions in the museum collection data than the sampling data. We expect this because of biases associated with museum collection data, specifically the "rare representation effect" where collectors target rare species (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010).

3. The majority of species missing from both datasets will be those that are narrowly distributed or habitat specialists, because these uncommon species are least likely to be noticed by collectors or sampled by systematic surveys.

Methods

Study Area

The country of Trinidad and Tobago is formed of two main islands lying to the northeast of Venezuela. Trinidad, the larger island, is 4820 km^2, and is only 11.3 km from Venezuela. Tobago is far smaller at 308 km^2, and sits 30.6 km from the coast of Venezuela. The climate of both islands is tropical, with a mean annual temperature of around 27°C, and a temperature range of around 17°C to 33°C. The islands support a variety of freshwater habitats. Streams in the north of Trinidad and in Tobago contain mostly clear, fast flowing water with firm substrate ranging from boulders to gravel. The more southern parts of Trinidad contain slower, more turbid streams, with substrates ranging from sand to mud.

Data Sources

Sampling was designed to provide useful data for conservation and management of the freshwater fish of Trinidad and Tobago. Ninety-one stream and river sites across the two islands were selected, representing all major drainages, biogeographic regions and river types. Each river had between one and three sampling locations. Sampling took place over two years (1997-1998), and 22 sites were sampled twice. Consistent sampling methods were used throughout, with small adjustments depending on stream type. Wherever possible, seine nets were used to block off sections of around 50m of river. A combination of methods including electrofishing (primarily in clear water), seine netting (in both clear and turbid water), and gill and trammel nets (particularly in larger rivers), were used to catch as many fish as possible in the blocked off sections. Species identities and their numerical abundances at each site were recorded before fish were returned to the stream at the point of capture.

The University of the West Indies Zoology Museum (UWIZM) is the de facto zoological collection for Trinidad & Tobago, and at the time of writing is one of the largest collections in the Caribbean. There are an estimated 70,000 specimens in the collections, the majority of which are local in origin. Although there was sporadic collecting of freshwater fish species from as early as 1936, the first significant fish collecting began in the mid-1960s and persisted through the rest of the 20th century. Few additions were made in the 2000s, but from 2010 onwards there were significant additions from work done by visiting researchers. The UWIZM data are open access, and available at https://doi.org/10.15468/m48ug8.

For our analysis, we use collection year as the collection unit of the museum data (Petersen & Meier, 2003). The nomenclature of the freshwater fish species in both the survey and the museum collection was also checked using the list of old and new species names provided by the species list and key of fish species (Phillip *et al*., 2013), ensuring that all names used in the final analysis were up to date and comparable.

Analysis

Freshwater fish species lists, particularly those for islands, typically include species that are mostly restricted to freshwaters, and taxa that are either normally found in estuaries as well as fish that are predominately marine but occasionally move upstream. In addition these lists typically include anadromous and catadromous species. Here we follow Phillip *et al*. (2013)'s definition of freshwater fish, based on habitat preference and taxonomy. To identify these freshwater fish, we used a recent literature review that includes a comprehensive species list and key for fish species (Phillip *et al*., 2013). From this list, we selected only species that are considered by Phillip *et al*. (2013) as truly freshwater, not those that are usually regarded as marine or coastal species. We included transient species but not species that Phillip *et al*. (2013) considered misidentifications. DATP also submitted specimens and records to the museum between 1997 and 1998 as part of her survey. To avoid any confounding influence of these records on the museum collection data results, we removed all samples collected by DATP in 1997 and 1998.

To estimate freshwater fish species richness in Trinidad and Tobago, we used rarefaction and extrapolation curves computed by the 'iNEXT' R package (Chao *et al*., 2014). Extrapolation enables the user to estimate the number of species that would be detected if sampling was increased to include an additional number of individuals or sampling units. In individual based rarefaction, individuals should be sampled at random (Colwell *et al*., 2012), an expectation that museum data (and most ecological surveys) will not satisfy. But sample-based incidence data need only be representative of the area surveyed, including spatial heterogeneity (Chao & Colwell, 2017; Colwell, Mao, & Chang, 2004). Nonetheless, rarefaction and extrapolation has been shown to be a robust and informative method with different types of data (e.g. phylogenetic diversity (Chao *et al*., 2015; Hsieh, Ma, & Chao, 2016b) and distributions of stone tools in Pleistocene North America (Buchanan *et al*., 2017). Also, note that the estimate attained from extrapolation is exactly the same as the non-parametric Chao2 estimate. For both datasets, we used the "incidence_freq" datatype option, that is sample-based rarefaction rather than individual based rarefaction. For sample-based rarefaction sampling units need only be representative of the sampling area, which is a less stringent assumption than for individual based rarefaction (Colwell *et al*., 2004). We therefore chose sample-based rarefaction rather than individual based rarefaction in both cases. For the Museum data, we used the year in which an acquisition was recorded as its sample id. We benchmarked the estimated species richness numbers against the number provided by a comprehensive species list collated using all available fish records and expert knowledge of the Trinidad and Tobago freshwater fish fauna (Phillip *et al*., 2013)

To further understand whether the survey dataset and the museum collection dataset differ in the types of fish they represent, we categorized each fish species by status (i.e. native/non-native), by habitat specificity, and by how widely it was distributed across Trinidad and Tobago, using information in Phillip *et al*. (2013) and FishBase (fishbase.org) - see Table 1 and Table S1. We compared the distribution of characteristics of the species observed in both the survey and museum datasets against the results of a null model (Fig. S1). The assumption of the null model was that each species had equal probability of being recorded, as long as it is found, or has been found, in the rivers of Trinidad and Tobago. For each iteration of the null model, 39 species (the number of observed species in the Museum data) were randomly selected from the list of 65 species that are likely to be present in Trinidad and Tobago according to Phillip *et al*. (2013). We recorded the native status, distribution, and habitat specificity of each of the randomly selected species, and then proceeded with the next iteration. The model had 1000 iterations. We then calculated the quantiles

of the observed numbers of fish in the survey and museum data for each category in relation to the null model results.

Table 13. Category descriptions for assigning species characteristics. Information was extracted from (Phillip et al., 2013). Any fish described as "mistake" were removed from the analysis during data preparation.

Designation	Description
Status	
No data	No data on this characteristic in the fish key
Introduced	Species colonised from a human introduction
Mistake	Misidentifications
Presumed native	Presumed native to Trinidad and Tobago
Recent Colonist	Natural colonists from the Orinoco River
Transient	Species not recorded in the last 2 to 3 surveys. They are natural colonists from the Orinoco River that did not become established
Habitat Specificity	
No data	No data on this characteristic in the fish key
Specialist	Lives in only one water type, i.e. clear and fast flowing
Generalist	Can live in different water types, i.e. clear fast flowing water and turbid water
Distribution	
No data	No data on this characteristic in the fish key
Narrow	Only found in a few sites
Intermediate	Either found in a subsection of Trinidad that is more than a few streams or fish described as "widely distributed" in a subsection of Trinidad
Wide	Found in most of Trinidad, or found in both Trinidad and Tobago, or described as "widely distributed"

Results

Estimated Richness

Visual inspection of the observed species richness accumulation curve for the survey data (Fig. 1a), suggests an asymptote is close. Although there are far more records overall in the survey data than the museum data (Table 2), most species are found at only a few sites (under 20) – a typical pattern in ecological surveys (Fig. 1c).

Table 14. A breakdown of the numbers of acquisition records uniques (species only recorded once), duplicates (species recorded twice), and the observed number of species in the sampling and museum freshwater fish, as well as the number of freshwater fish estimated to be extant in Trinidad and Tobago according to rarefaction and extrapolation using iNEXT. These species richness estimate are exactly that of the non-parametric Chao 2 estimate.

Dataset type	Acquisitions	Sampling Units	Uniques	Duplicates	Species Observed	Species Richness estimate	Lower bound	Upper bound
Survey	21153	56	4	3	38	50 (+/- 17)	40	131
Museum	785	30	2	3	39	46(+/- 6)	40	68

In contrast to the survey data results, the museum data accumulation curve does not support an asymptote close to the 39 species recorded (Fig. 1b). Collection effort is extremely variable in the museum data, with over 200 records submitted for one year in the 1990s and fewer than 100 for most other years (Fig. 1d). There is, however, no noticeable increase in new species during the period of increased specimen submissions (Fig. 1b). In addition, both data collection methods provide samples that are close to completely representative (Fig. 1e & 1f).

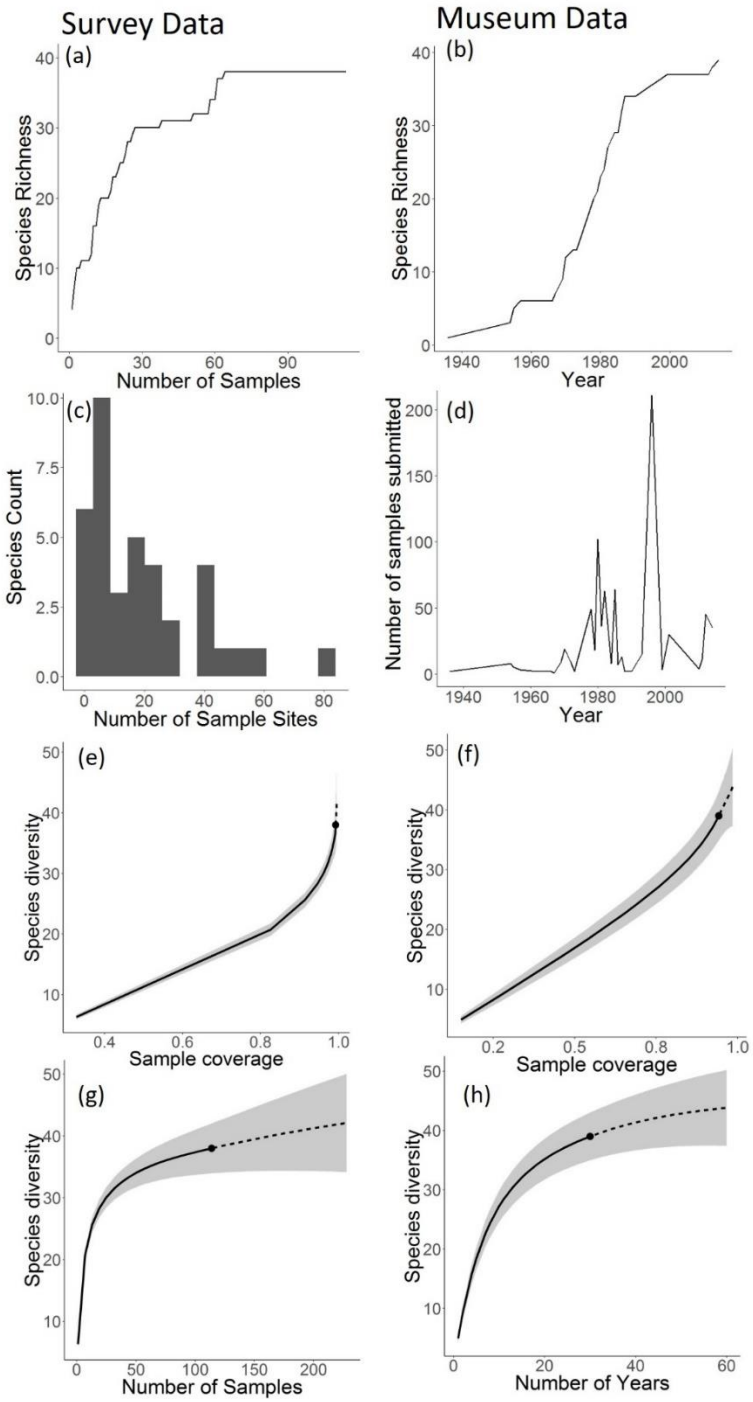

Figure 1. Plots of the Trinidad and Tobago freshwater fish targeted survey data and museum collection data. Plot (a) is the accumulation of species richness as new sites were added to the survey data in terms of the actual temporal sequence of data collection. Plot (b) shows the accumulation of species richness in the museum collections through time. Plot (c) shows the frequency of species found in multiple sites, and plot (d) shows the unequal distribution of sample submissions to the museum collection over time. Plots (e) and (f) show the coverage-based extrapolation for the survey and museum data respectively, and (g) and (h) show the estimated species richness of the survey and museum data, respectively, using the iNEXT sample-based extrapolation. The grey ribbon represents the 95% Confidence Intervals of the estimates.

The iNEXT extrapolations estimated were within 10% of each other (50 species for the survey data (Fig. 1g), 46 for the museum data (Fig. 1h)), and they both lie well within each other's upper and

lower 95% confidence intervals (Table 2). The survey data had higher uncertainty around this estimate, with the upper 95% richness estimated as 130 species as opposed to the 68 estimated from the museum data. The range of estimates predicted by both data types included the 65 species reported by the comprehensive key and species list (Phillip *et al*., 2013) (note the 66 quoted in the text of (Phillip *et al*., 2013) is a miscount of the true number listed in the table of species).

Assemblage composition

Fewer species are missing from the museum data but recorded in the survey data (4) than recorded in the survey but missing from the museum data (6) (Fig.2). No transient species were recorded in either dataset (Table 3), and the majority of species in both datasets were native. A high proportion of species missed by both data collection methods either were data deficient, transient, narrowly distributed or habitat specialists (Table 3).

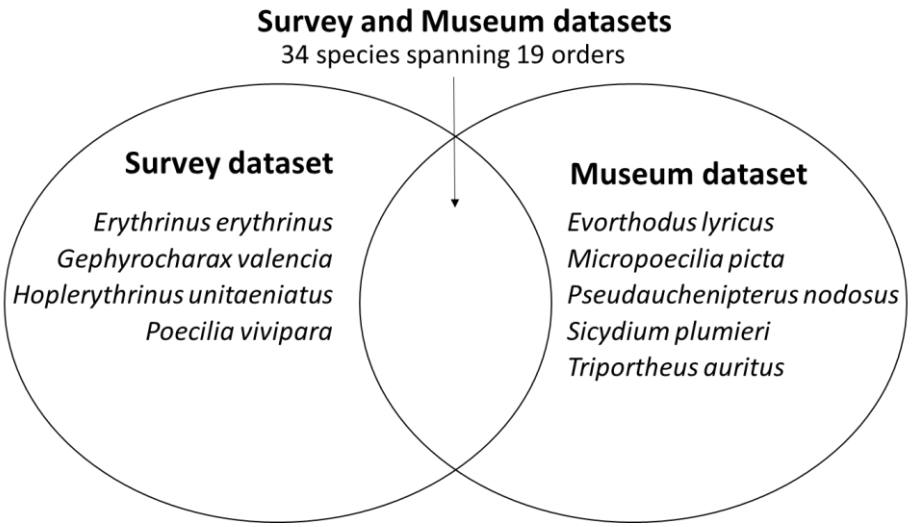

Figure 2. A breakdown of which species were recorded only in the survey data and only in the museum data. The majority (34) species were recorded in both datasets. For a complete list of which species where found in each dataset see Table S1.

Contrary to our expectation, there were no biases evident between types of fish recorded in the survey and museum data (Table 3; Fig. 3). Both underestimated the number of species thought to be present in Trinidad and Tobago, but the fraction of native species was higher in both cases than in the overall list provided by Phillip *et al*. (2013). Both datasets also included more intermediately or widely distributed species than this overall list, although the difference was more marked in the museum data than the survey data. There are also more habitat generalists in the observed data (both methods) than expected if they were a random draw from the overall list. This difference, however, is less pronounced because the number of habitat generalists in both surveys fall within the 95% quantiles of the null model.

Table 15. A breakdown of the status, distribution and habitat preference characteristics of all freshwater fish species in Trinidad and Tobago as stated in (Phillip *et al*., 2013). A further breakdown of the characteristics of the fish found in the survey and museum datasets is also included, and the quantiles of these values in relation to the null model results. Finally, we include a breakdown of the characteristics of the fish found in neither the Survey nor the Museum data.

		All Species	Survey	Museum	Survey Quantile	Museum Quantile	Not found
Status	No data	3	0	0	0.18	0.18	3
	Introduced	5	2	2	0.42	0.42	3
	Native	53	33	34	1.00	1.00	16
	Recent Colonist	4	3	3	0.92	0.92	0
Distribution	No data	11	0	0	0.00	0.00	11
	Narrow	13	6	4	0.34	0.05	6
	Intermediate	24	19	22	1.00	1.00	2
	Wide	17	13	13	0.99	0.99	3
Habitat	No data	2	0	0	0.00	0.00	2
	Specialist	23	14	14	0.84	0.84	7
	Generalist	40	24	25	0.94	1.00	13

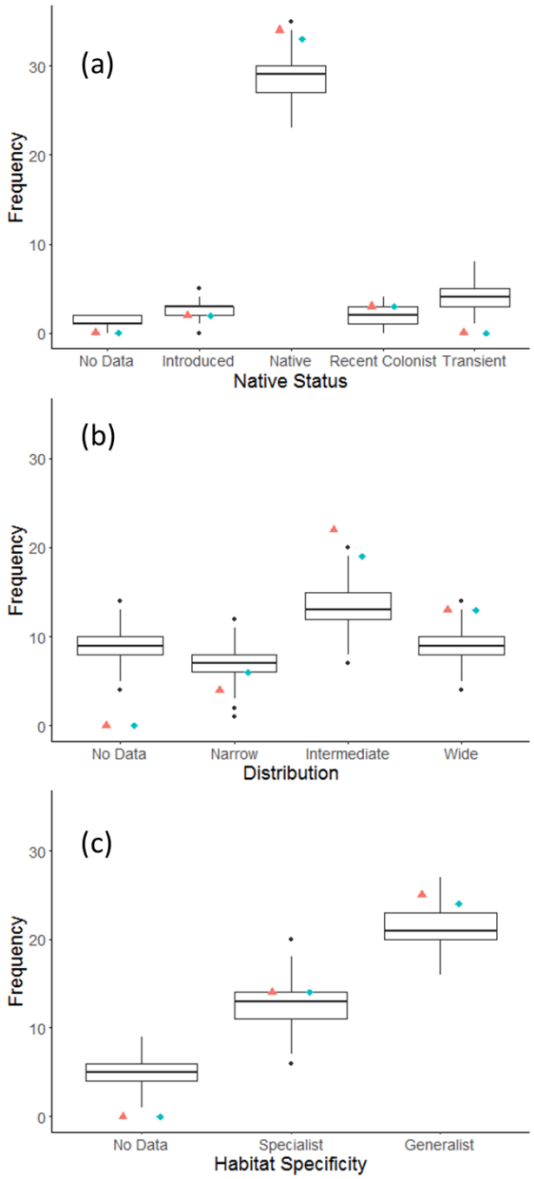

Figure 3. The native status (a), distribution (b) and habitat specificity (c) of 39 fish randomly selected by a null model with 1000 iterations (black boxplots), compared to the observed habitat specificity of species found in the survey data (red triangles) and museum data (blue diamonds). Box plots show medians, upper and lower quantiles and outliers. A violin plot showing the observed values and the sampling distribution of the model can be found in Fig. S2.

Discussion

Despite the two orders of magnitude fewer records contained in the museum data than the targeted survey data, both datasets provided comparable estimates of regional freshwater fish species richness in Trinidad and Tobago. The richness estimates of the museum and survey data were within 10% of each other (50 species and 46 species, respectively), and there was a large overlap (85%) of species identified. Both estimates fall 20% below the maximum number (65) of species potentially present according to the exhaustive list (Phillip *et al*., 2013; Table 2), but the upper confidence intervals of the estimates are inclusive of this maximum number of potential species.

We expected differences in the composition of species observed in the two contrasting datasets because of biases in the collection methods of the museum data. For example, sampling in historical museum collections generally occurs *ad hoc* by a variety of uncoordinated collectors, typically leading to an overrepresentation of easily accessible areas and centres of population (Engemann *et al*., 2015; Guralnick & Van Cleve, 2005; Soberón, Llorente, & Oñate, 2000; Tobler, Honorio, Janovec, & Reynel, 2007). Another bias is the "rare representation" effect: the tendency for collectors to favour unusual species, combined with longer collection times, giving a greater likelihood of finding species outside of their usual ranges (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). The rare representation effect could cause overestimations of species richness, which in turn might inflate the importance of transient species that do not contribute to ecosystem processes. Contrary to our expectations, we found a striking similarity between the identities of the species recorded in the survey and museum data (Figs 55 & 3), suggesting these biases do not strongly influence regional species richness estimates in these data. The majority (85%) of species were recorded in both datasets. In addition, there was no indication of biases in types of species recorded; the museum collection data did not contain more transient species, nor habitat specialists or narrowly distributed species, than the survey data.

Our results suggest that, although collection methods differ considerably between datasets, survey and museum data can provide comparable estimations of the regional assemblage species composition. The substantial overlap in species present in both datasets is particularly notable because the dissimilarity between samples is inflated by incomplete species lists (Chao, Chazdon, Colwell, & Shen, 2005). Consequently, historical museum collection data are potentially useful for analysing other aspects of biodiversity change in addition to richness. Rates of turnover of species identity within assemblages, for instance, could be assessed with species lists. Rates of turnover are variable and driven by a complex collection of biotic and abiotic factors (Korhonen, Soininen, & Hillebrand, 2010), and warrant more analysis. Datasets such as the collections held at The University of the West Indies Zoology Museum, Trinidad, could serve as a baseline for furthering our understanding of turnover within communities. Within the Caribbean region, for instance, collections similar to those held by The University of the West Indies Zoology Museum, Trinidad, include those held at The National Zoological Collection of Suriname (NZCS) and The Museo Nacional de Historia Natural ¨prof. Eugenio de Jesus Marcano¨ in Santo Domingo, Dominican Republic. More widely, there are similar museums with extensive collections that could be used to form the basis of species lists in Costa Rica, Cuba, Venezuela, Colombia, Panama and Nicaragua. There are also increasing possibilities for searching for and combining collections from multiple sources as more museum collection data are uploaded onto online repositories like the Global Biodiversity Information Facility (GBIF), meaning collections held outside of tropical regions can also be harnessed for creating baseline species lists.

Surveys provide robust data on species distributions and abundance, and are generally suitable for a wider variety of analyses than museum data. For example, the combination of species identity and relative abundance values of systematic survey data mean diversity metrics such as Hill numbers (which include forms of Shannon and Simpson diversity measures) can be calculated (Hill, 1973). These estimates allow the almost unbiased "effective" number of frequent species within assemblages to be estimated (Hsieh, Ma, & Chao, 2016a). However, surveys are not practical in many cases. Undertaking surveys can be expensive and requires good access to expertise and sites. The survey we used in this analysis took place over two years, and involved many hours of preparation and field work. Even in relatively well sampled sites, a short period of sampling activity

does not often come close to the actual number of species in an area (Fattorini, 2013). This is a particular problem in tropical regions, where there is a substantial need for data. Alternative data gathering exercises, namely intensive local sampling areas (i.e. Bouchet, Lozouet, Maestrati, & Heros, 2002; Brown *et al*., 2018; Longino *et al*., 2002) could also be useful, but these sampling endeavours also require extremely high levels of expertise and investment, which are often unavailable, and are not practical on a regional scale. In these cases, museum and other historical natural history collections provide a useful resource for estimating regional species richness. This is not to say that historical museum data can or should replace systematic survey. For instance, an aspect of biodiversity change that may strongly affect ecosystem functioning is reordering of species abundances with assemblages (Jones, Ripplinger, & Collins, 2017). To what extent such reordering of community structure, in particularly whether dominant species are changing identity, requires representative relative abundance data, which cannot be extracted from *ad hoc* museum collections.

While both datasets investigated in this study gave similar estimates of species richness and assemblage compositions, there was substantial divergence between their estimates and that of a recent literature review and key (Phillip *et al*., 2013; Table 3). The species missed from both datasets tended to be narrowly distributed habitat specialists or recent additions to the Trinidad and Tobago freshwater fauna, and may include some species that were presumed native but may not be currently present in the region. Such biases are extremely common in ecological assemblage data (Longino *et al*., 2002), with most undescribed species believed to be narrowly distributed and uncommon within their home ranges (Pimm *et al*., 2014). These biases raise the question of whether both our empirical datasets underestimate species richness, or whether the exhaustive list compiled from a literature search is an overestimate. This is an important consideration, because how much emphasis is given to the most difficult to detect species in an assemblage heavily influences estimated extinction and turnover rates. Recently detected species may go extinct before or just after their discovery (Barnosky *et al*., 2011; Lees & Pimm, 2015), particularly if they are transient species (Magurran & Henderson, 2003) or have restricted distributions (Pimm *et al*., 2014).

Concluding remarks

Uncertainty around biodiversity levels and distribution hinders our understanding of key biodiversity statistics and consequently our ability to make informed conservation decisions (Pimm *et al*., 2014). Understanding the information gaps around biodiversity knowledge is essential for progression of the field (Hortal *et al*., 2015). In our analysis we demonstrated that both historical museum collection data and survey data can provide useful regional species richness estimates to use as baselines for assessing biodiversity change. Both datasets also provided comparable estimates of the identities of species within the assemblage, as they detected all but the transient or very difficult to detect species. Most assemblages display similar species abundance distributions, characterised by both common and rare species (McGill *et al*., 2007) and often include both “core” and “transient” species (Magurran & Henderson, 2003; Taylor, Evans, White, & Hurlbert, 2018). Our results suggest that the majority of a region’s “core” species are detected by both museum data and survey data to similar extents. Consequently, species lists for assessing turnover within tropical regions, and amongst these “core taxa”, could be compiled from existing historical museum collections where suitable systematic survey data are unavailable. This would provide opportunities for monitoring and understanding biodiversity change within tropical regions that otherwise lack appropriate baseline data.

Then again, it is difficult to verify which of the fish species potentially in Trinidad and Tobago are actually present in the region at a given time. This uncertainty needs to be taken into account in baseline estimates of regional species richness and turnover/extinction analyses.

Based on our results, and with appropriate caveats, we therefore recommend increased use of historical museum collections, particularly those containing tropical data, in assessments of regional biodiversity. These data are more readily available than intensive systematic survey data in many parts of the world, and assemblage composition within such collections can be sufficiently unbiased as to serve as useful baselines for assessing temporal turnover of species identities. By harnessing their full potential, we can provide a useful source of biodiversity information to help bridge the knowledge gap between temperate and tropical systems.

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Gradients in predation risk in a tropical river system

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Abstract

The importance of predation risk as a key driver of evolutionary change is exemplified by the Northern Range in Trinidad, where research on guppies living in multiple parallel streams has provided invaluable insights into the process of evolution by natural selection. Although Trinidadian guppies are now a textbook example of evolution in action, studies have generally categorised predation as a dichotomous variable, representing high or low risk. Yet ecologists appreciate that community structure, and the attendant predation risk, varies substantially over space and time.

Here, we use data from a longitudinal study of fish assemblages at 16 different sites in the Northern Range to quantify temporal and spatial variation in predation risk. Specifically we ask: a) Is there evidence for a gradient in predation risk? b) Does the ranking of sites (by risk) change with the definition of the predator community (in terms of species composition and abundance currency) and c) Are site rankings consistent over time?

We find compelling evidence that sites lie along a continuum of risk. However, site rankings along this gradient depend on how predation is quantified in terms of the species considered to be predators and the abundance currency is used. Nonetheless, for a given categorisation and currency, rankings are relatively consistent over time. Our study suggests that consideration of predation gradients will lead to a more nuanced understanding of the role of predation risk in behavioural and evolutionary ecology. It also emphasises the need to justify and report the definition of predation risk being used.

Keywords: Gradients; Predation risk; Trinidadian guppy; *Poecilia reticulata*; Trinidad; Abundance currency.

Introduction

Rivers are defined by gradients, with abiotic conditions changing from their upper to lower reaches in a predictable manner. Abiotic gradients are easily quantified and widely used to help predict and explain the ecology of freshwater communities (Vannote *et al*., 1980). However, biological elements, such as species richness and predation pressure, are also non-random features of the system that can be usefully employed to explore other ecological and evolutionary patterns (Beecher *et al*., 1988; Gilliam *et al*., 1993; Jackson *et al*., 2001; Reimchen, 1994). In parallel with the physical conditions of the continuum, these biological gradients run from upstream stretches, which typically have lower species richness and lower predation pressure, to downstream stretches where species richness and predation pressure are almost always higher (Matthews, 1998). Explanations for these gradients include dispersal limitation due to waterfall barriers, preventing some species from colonising upstream regions, as well as habitat characteristics such as water depth, which may be too shallow in higher reaches to support larger species (Harvey and Stewart, 1991).

Predation pressure can have a profound effect on the structure and composition of aquatic communities (Jackson *et al*., 2001; Matthews, 1998). The Northern Range of Trinidad has played an important role in helping us understand the role of predation in natural ecosystems. Identified as a 'natural laboratory' in the 1940s (Haskins, 1961), over the past 60 years studies on guppy (*Poecilia reticulata*) populations living in Trinidad's multiple parallel streams have provided invaluable insights into evolutionary ecology (e.g. Liley and Seghers, 1975; Magurran *et al*., 1992; Reznick *et al*., 1990). Indeed, some of the best evidence for evolution by natural selection has emerged from semi-natural experiments using this system. Most notably, this work includes some of the first experimental demonstrations of evolution on the timescale of years (rather than millennia) and in a vertebrate (rather than bacteria in a petri dish) (e.g. Endler, 1980; O'Steen *et al*., 2002; Reznick *et al*., 1997).

Gradient vs Dichotomy

One of the reasons the Northern Range has been so fruitful in terms of evolutionary research is that some of its parallel streams are interrupted by waterfalls, which can be tens of metres high and thus prevent the upstream dispersal of certain fish species. Guppies have successfully colonised many of the above-barrier sites, and these are considered 'low risk' from the guppy's perspective, as typically only the killifish (*Anablepsoides hartii,* formerly called *Rivulus hartii*) also exists here. In contrast, those below waterfalls are regarded as 'high risk' because guppies living there find themselves cohabiting with larger predatory species, including the pike cichlid *Crenicichla frenata* (formerly called *C. alta*) and the wolf-fish or 'guabine' *Hoplias malabaricus*. The advantages of this 'barrier waterfall' phenomenon to evolutionary study was first noted in the 1950s (Haskins and Haskins, 1951) and since then the 'high' versus 'low' dichotomy has helped scientists link differences in predation risk to differences in a huge range of traits, including size, behaviour (Liley and Seghers, 1975), colouration (Endler, 1980) and numerous life history traits (Reznick and Endler, 1982).

Traditionally, guppy research has emphasised the contrast between the extremes in this system. However, as most researchers are aware, there are finer scale differences in guppy traits along gradients of predation pressure in these rivers (Gilliam *et al*., 1993; Torres Dowdall *et al*., 2012). To understand how subtle differences in local conditions influence evolutionary outcomes we first need to be able to properly quantify the expected predation gradient. We also need to be aware that using different categories of predation pressure potentially influences the ranking of sites.

Predation Categorisation

Most studies into guppy adaptation to predation do not quantify the predation pressure as such, but instead characterise different sites according to which species are found there (presence/absence), either historically, or at the time of sampling. Endler (1978) classified six 'types' of predator

assemblage. However the two species that most researchers pay attention to are the wolf fish *H. malabaricus* and the pike cichlid *C. frenata* (Farr, 1975).

A limitation of this approach is that we know that many other species also predate on guppies, even if to a lesser degree (Seghers, 1973). Even the cohabitant most closely associated with 'low' predation sites, *A. hartii*, is known to consume juvenile guppies (Mattingly and Butler, 1994). A key issue, therefore, is deciding which species to consider as potential predators. Despite many decades of research on this system, guppy predators have yet to be systematically ranked in terms of their actual risk to a guppy. Fortunately, we do have some information on trophic level and feeding mode which allows us to assign the fish occurring in an assemblage to categories based on the degree of risk they likely pose (Kenny, 1995; Phillip *et al*., 2013)

Even once justification has been made for which species 'count' as predators, the next question is should these be quantified in terms of their numerical abundance or their biomass? Different abundance currencies provide different insights in community ecology (Magurran, 2004). In general, biomass is more commonly used in aquatic systems, and numerical abundance in terrestrial studies. Numerical abundance is widely used to explore community dynamics, while biomass may be a better indicator of resource allocation (White *et al*., 2007). Although some studies treat these abundance currencies as interchangeable (Taper and Marquet, 1996a), this is not necessarily the case in taxa, such as fish, where body size varies considerably amongst species and through ontogeny (Mittelbach *et al*., 1988). It is important to ask, therefore, whether our perception of where sites lie on a gradient of risk depends on the abundance currency being used.

Temporal dynamics

A final consideration is that aquatic assemblages are not static, and any survey to assess predator numerical abundance or biomass is just a snapshot of a dynamic system. Indeed, temporal turnover is a feature of all ecological communities (Magurran and Henderson, 2010). Thus far, relatively little attention has been paid to the temporal dynamics of the Northern Range system (Magurran, 2005). For example, we know that both guppy density (Grether *et al*., 2001; Magurran, 2005; Reznick, 1989) and sex ratio (Pettersson *et al*., 2004) vary considerably over time, yet we understand very little about how these, or other patterns, may be related to temporal changes in the dynamics of predatory species.

Aims

Using data from 16 sites across eight different rivers along the southern slopes of the Northern Range collected over a six year period, we seek to evaluate the potential of the biological gradient of predation pressure in the Northern Range as an alternative to the more commonly applied high-low predation dichotomy. We categorise predation pressure into three levels – narrow, intermediate, and broad, using published assessments of the diets of Trinidadian fish species (See Table 1). We use this categorisation to, first, examine the evidence for a gradient in predation risk in this system. We do this by plotting site trends in predation pressure for each category and for two abundance currencies (numerical abundance and biomass). Next, we ask if site rankings shift across predator categories within currency, and across currency within predation categories. Finally, we assess the degree of temporal consistency in site rankings when predator category and currency are held constant.

Methods

Data collection

Sixteen sites in Trinidad's Northern Range were sampled once a year (July/August) for six years (2011-2016). These sites are spread between 8 different rivers along the Southern slopes of the Northern Range, and each consists of a 50 metre stretch of stream (Figure 1).

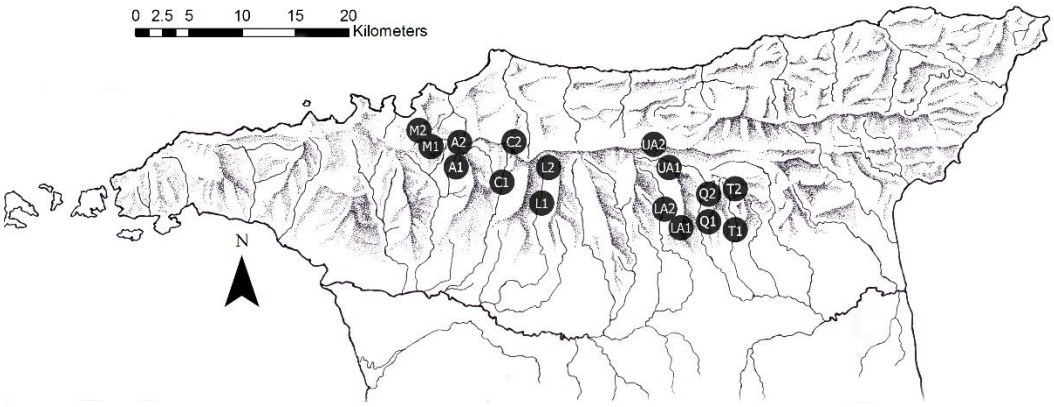

Figure 1. Map showing the location of the 16 sites across Trinidad's Northern Range. Site abbreviations are as follows: A1: Acono site 1; A2: Acono site 2; C1: Caura site 1; C2: Caura site 2; L1: Lopinot site 1; L2: Lopinot site 2; LA1: Lower Aripo site 1; LA2: Lower Aripo site 2; M1: Maracas site 1; M2: Maracas site 2; Q1: Quare site 1; Q2: Quare site 2; T1: Turure site 1; T2: Turure site 2; UA1: Upper Aripo site 1; UA2: Upper Aripo site 2.

Sampling involved blocking the stretch at either end using seines, before fishing with a two-person seine net, followed by electrofishing. Dip nets were also used in the shallows. All fish were identified to species, and weighed individually to the nearest gram, with the exception of guppies, which were too small to be weighed in the field, and were instead noted as mature female, mature male or juvenile (typical weights were then used to estimate biomass for this species). On occasions where fish were seen but not caught, length was estimated and an appropriate length-weight curve consulted to give an estimate of biomass (see Deacon *et al*., 2017 for more details).

Analyses

We used three alternative categories of predation, based on trophic classifications using available information on diet (Kenny, 1995; Phillip *et al*., 2013) . The first takes a 'narrow' view of what a guppy predator is, including only two 'strongly piscivorous' species widely acknowledged to be the main predators of guppies: *Hoplias malabaricus* and *Crenicichla frenata*. The second 'intermediate' view includes an additional two species that are considered 'moderately piscivorous'. Finally the 'broad' view encompasses even those fish classified as 'weakly piscivorous' (Table 1).

Table 1: Species of predator included in each category. Note that *Crenicichla frenata* was formerly called *C. alta*; *A. hartii* was formerly called *Rivulus hartii*, and *Andinoacara pulcher* was formerly called *Aequidens pulcher*. 'Narrow' includes only the two most strongly piscivorous species, 'intermediate' includes an additional two moderately piscivorous species, and the broad category includes all piscivorous fish in the system.

Scientific name (and authority)	Common name	Narrow	Intermediate	Broad
Crenicichla frenata Gill 1858	Pike cichlid	X	X	X

Hoplias malabaricus (Bloch 1794)	Wolf fish/Guabine	X	X	X
Anablepsoides hartii (Boulenger 1890)	Hart's killifish		X	X
Gymnotus carapo Linneaus 1758	Cutlass fish/ Knifefish		X	X
Agonostomus monticola (Bancroft 1834)	Mountain mullet			X
Andinoacara pulcher (Gill 1858)	Blue acara/ Blue coscorob			X
Cichlasoma taenia (Bennett, 1831)	Brown acara/ Brown coscorob			X
Corynopoma riisei Gill 1858	Swordtail sardine			X
Hemigrammus unilineatus (Gill 1858)	Featherfin tetra			X
Rhamdia quelen (Quoy & Gaimard 1824)	River Catfish/Silver catfish			X

Assuming that predation risk depends both on the presence and its abundance of predators, the predation pressure of each site was calculated for six different scenarios: narrow, intermediate and broad predation categories, and for the two abundance currencies - numerical abundance and biomass. Numerical abundance was defined as the total number of individuals of the species in a given category, summed over the year's sampling. Biomass was the total wet weight (g) of all individuals of the species in a given category . All analyses are based on these annual abundance data, and took place in R 3.3.2 (R Core Team 2016).

We first constructed box plots for each of the six scenarios based on mean annual predation values for each site. We used $\log_2$ numerical abundance and $\log_2$ biomass respectively to depict predator abundance, and positioned sites along the x-axis in order of predator abundance. The goal of these plots was to assess if the sites lie along a gradient or represent a dichotomy; the former would be represented by a continuum of sites, ranging from high to low, and the latter by distinct groupings of sites. The plots also allowed us to ask if some categories provide stronger evidence for a gradient than others.

Next we constructed tanglegrams (using the plot() function in R) to visualise the consistency in site ranking by predator category and abundance currency, and quantified this consistency using a Spearman's rank correlation test to compare the rankings. Sites were ordered in terms of decreasing mean predator abundance over the entire 6-year sampling period, with the sites with the highest values at the top of the tanglegram.

Finally, using linear models we plotted the trend (predator abundance against year) for the 16 sites using the six approaches (three categories using numerical abundance and three categories using biomass). We evaluated the temporal consistency of site rankings within each predator category and currency using a Kendall concordance test (the kendall.global function in the R package vegan (Oksanen *et al*., 2007)).

Results

Gradient v. dichotomy

Plots of log numerical abundance and biomass illustrate how the 16 sites capture the gradient of predation risk over space (Figure 2). The narrow category of predation separates out the two lowest predation sites (UA1 and UA2; see Figure 1) while all other sites fall on a continuous gradient.

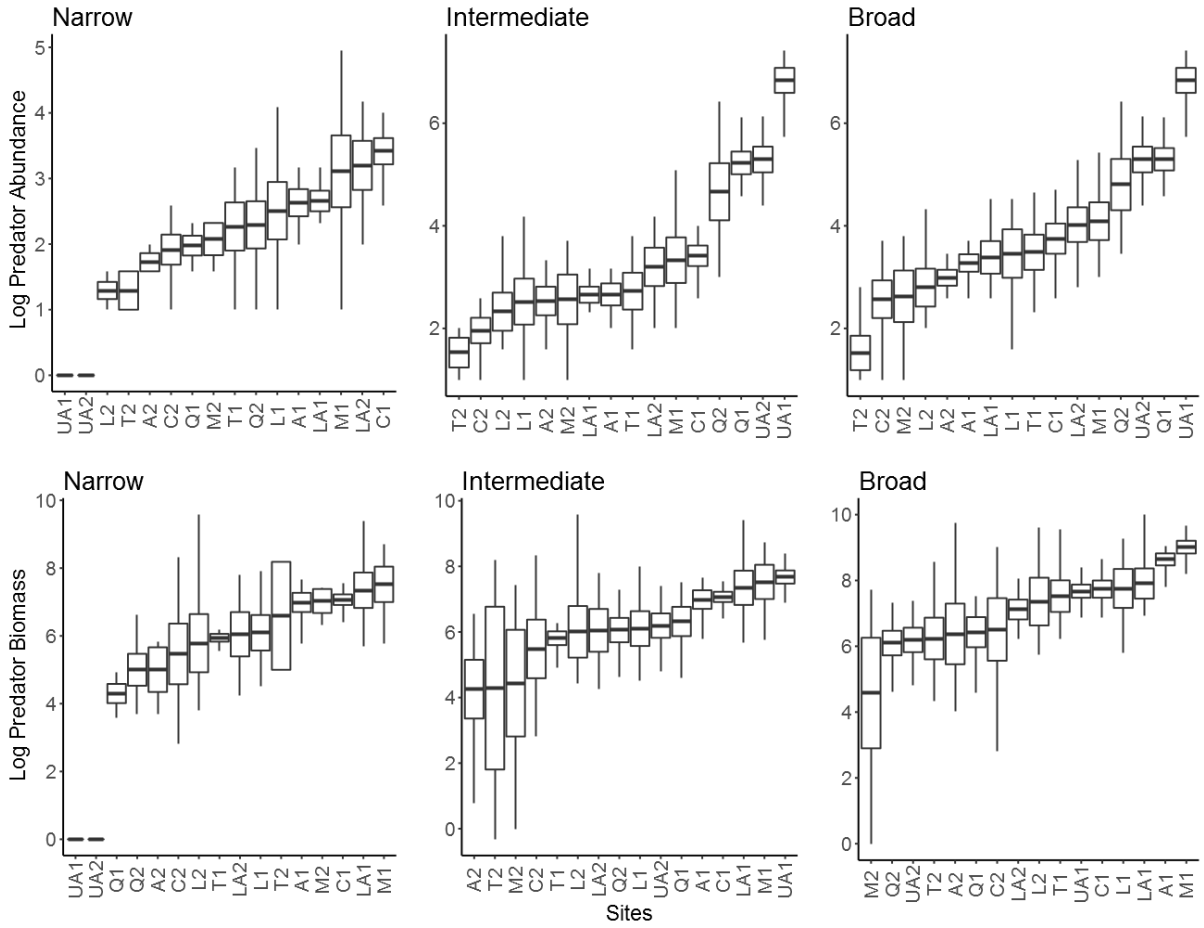

Figure 2. Mean values, standard errors (boxes) and ranges (whiskers) for six time points for each site, for log predator numerical abundance (upper row) and log predator biomass (lower row) for the three categories of predators (Narrow, Intermediate and Broad). Sites are plotted in rank order along the x-axis. See Figure 1 for key to the site codes.

Predation Categorisation

When quantifying predation using numerical abundance of individuals, site rankings shift across the predation categories. Specifically, the ranking of sites differs greatly depending on whether the narrow category of predators is used as opposed to the intermediate. There is no significant correlation between the rankings of narrow and intermediate numerical abundances ($r_s = 0.06$; $p=0.824$) or between narrow and broad ($r_s = 0.12$; $p=0.660$). Note the switch from lowest to highest ranked for the Upper Aripo sites between narrow and intermediate rankings. In contrast, the intermediate and broad categories rank the sites similarly and are highly correlated ($r_s =0.96$; $p<0.001$) (Figure 3A).

The ranking of sites is similar across predation classifications if biomass is used to quantify predator abundance, with significant correlations in all cases (Narrow+Intermediate: $r_s = 0.52$, $p = 0.039$; Intermediate+Broad: $r_s = 0.56$, $p = 0.025$; Narrow+Broad: $r_s = 0.70$, $p = 0.002$) (Figure 3B).

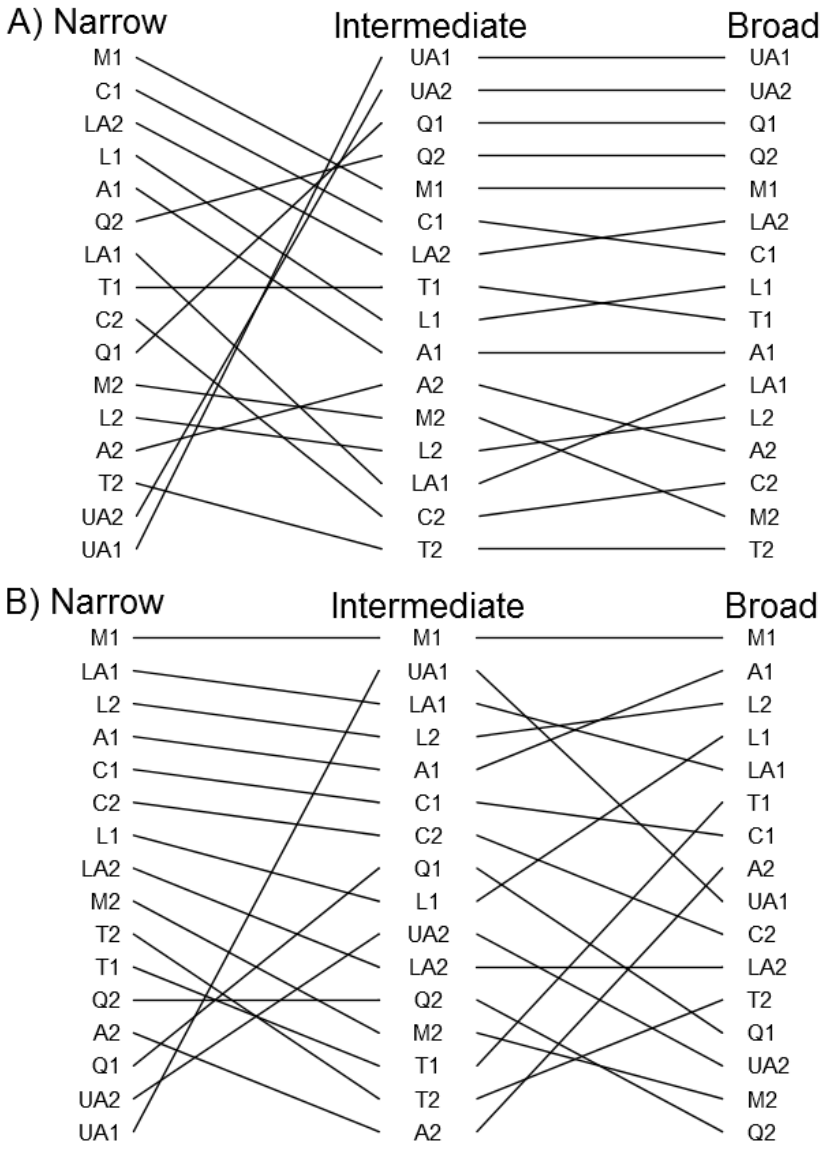

Figure 3: Tanglegrams comparing rankings of sites by mean predation risk, depending on whether a narrow, intermediate or broad category of predator assemblages is applied and whether A) numerical abundance and B) biomass is used as currency. See Figure 1 for key to the site codes.

By comparing numerical abundance and biomass side by side for each category of predation, we can see more clearly how the currency used affects how sites are ranked.

Sites are ranked consistently irrespective of abundance currency for the narrow category of predation (r_s=0.65; p<0.007) (Figure 4A). In contrast, when the intermediate or broad categories of predation are used, there is no significant correlation of site rankings between numerical abundance and biomass (Intermediate: r_s=0.21; p=0.443; Broad: r_s=-0.11; p=0.680) (Figure 4B+C).

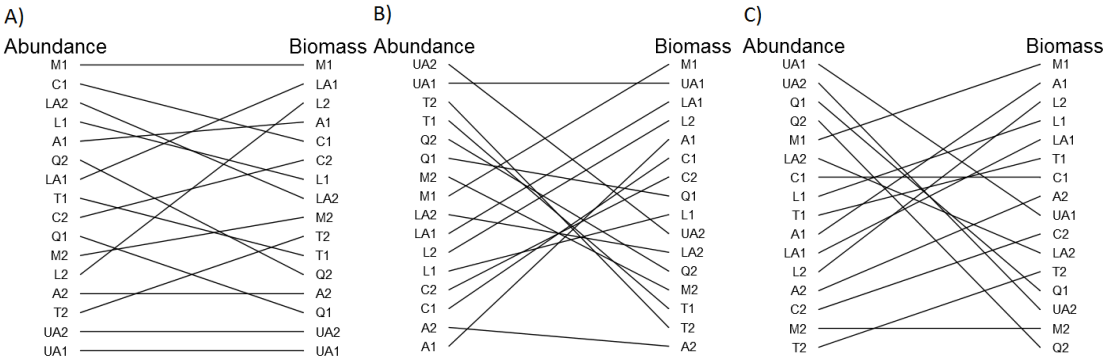

Figure 4: Tanglegram comparing how sites are ranked depending on whether mean biomass or numerical abundance are used to quantify predation, using the A) narrow, B) intermediate and C) broad categories of predation. See Figure 1 for key to the site codes.

Temporal Dynamics

Considerable variation in predator abundance exists over time within sites for all categories and currencies of predation. Different sites show different trends but in general the site rankings remain consistent over time regardless of the approach to quantifying predation pressure (Figure 5). This is reflected in significant Kendall concordance scores for rankings over time for all approaches, with the exception of when biomass and the intermediate category of predation are used to rank the sites. Numerical abundance does a marginally better job at ranking the sites consistently over time than biomass, with greater concordance coefficients for all categories.

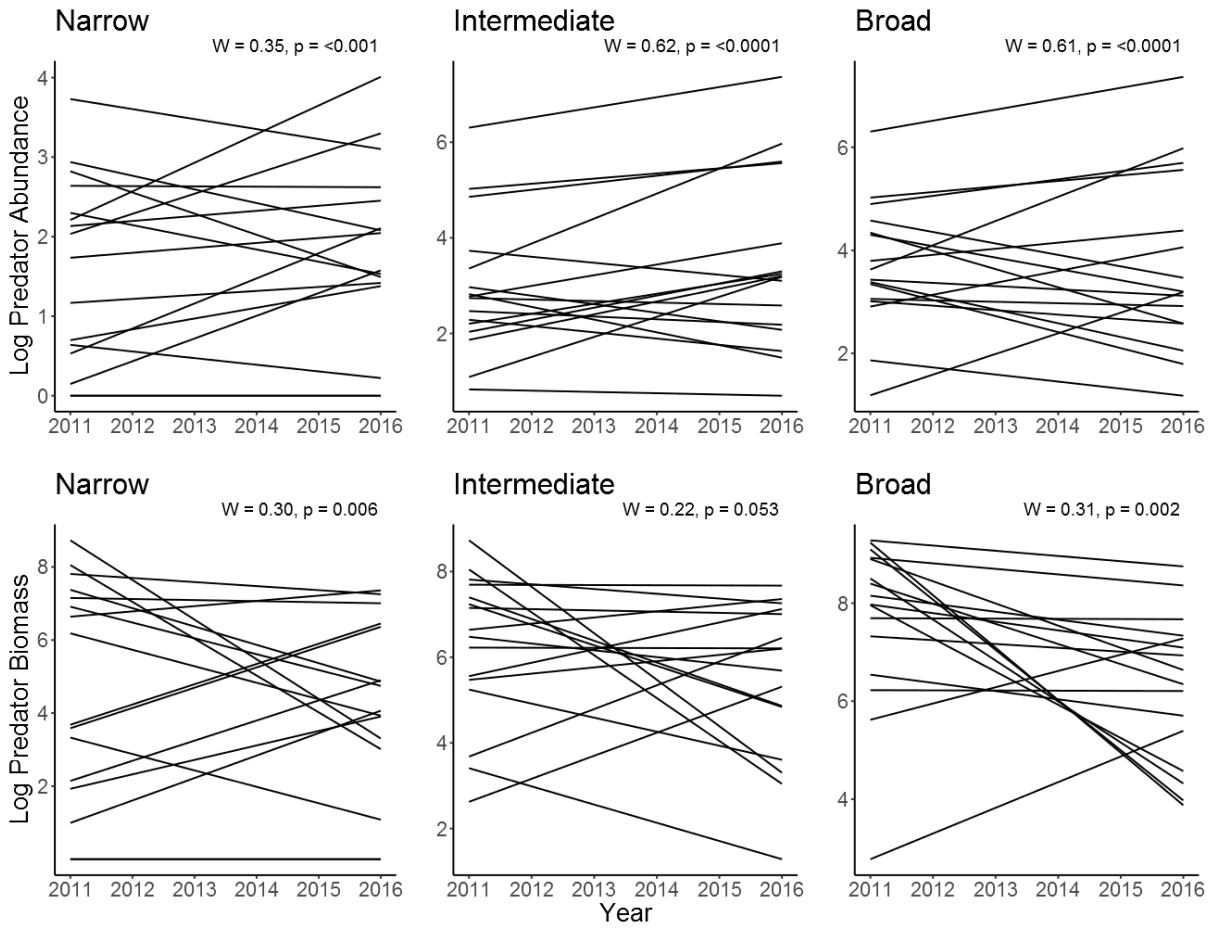

Figure 5: Trends over time for sites based on ranks per year for log_2 numerical abundance and log_2 biomass, as calculated according to the three categories of predation. Each trend line represents a site. Kendall Concordance Coefficients (W) and p-values are given for each plot.

Discussion

We find compelling evidence that, in terms of risk to guppy populations, river sites across the Northern Range of Trinidad lie along a continuum of predation risk. We further show that site rank along this continuum is broadly maintained over time. However, we also find that where a particular site lies on this gradient depends on how the predator assemblage is defined.

Gradient vs Dichotomy

Despite the expectation that biotic gradients (including predation intensity) parallel abiotic ones in river systems (Vannote *et al*., 1980), few studies have utilised the gradient concept when asking questions about evolutionary ecology in streams (although see Jourdan *et al*., 2016). Dichotomous contrasts, pitching high risk against low risk, have been widely employed. Many of the most famous examples are from Trinidad's Northern Range streams, a disproportionate number of which represent huge strides in our understanding of evolutionary ecology (e.g. Endler, 1980; Magurran *et al*., 1995; Reznick and Endler, 1982, to name just a few). This approach has the advantage of highlighting the stark differences in behaviour, physiology and ecology associated with habitats that offer sharp contrasts in risk.

After five productive decades focusing on the 'high-low' dichotomy, a study in in 2012 confirmed that the Guanapo River represents a useful gradient of predation pressure for investigations of guppy life history evolution (Torres Dowdall *et al*., 2012). The nature of predator communities for the Guanapo was defined in the early 1990s, when Gilliam *et al*. (1993) mapped the presence of different fish assemblages along its length. Torres Dowdall *et al*. (2012) linked this biological gradient to a fine scale pattern of variation in terms of guppy life history traits, moving beyond the traditional dichotomy to add nuance to our understanding of the effects of predation risk on guppy evolution. Our results show that this gradient is apparent between as well as within stream systems. As such it emphasises the need for careful and consistent quantification of predation pressure.

Our data show that sites do not form discrete clusters, but rather fall along a continuum of predation risk. This is true irrespective of the abundance currency or predator category used. Temporal variation means that sites exhibit overlap in predation pressure over the time frame of this study. The one exception occurs for the narrow predation category (regardless of currency): due to the barrier waterfalls some sections of stream (in this case two Upper Aripo sites) never support either of the main guppy predators, therefore these extreme low predation sites are separated from other sites. Numerical abundance appears a better discriminator of sites along this gradient than biomass (see Figure 2).

Although our sites were not selected *a priori* to represent the dichotomy within each river, the Upper and Lower Aripo sites (UA1, UA2, LA1, LA2) do comprise a typical and well-used dichotomous pair. The Upper Aripo is a frequently utilised 'low predation' river, while the Lower Aripo is a commonly sampled 'high predation' river (e.g. Botham *et al*., 2006; Magurran and Seghers, 1990). Using the narrow classification of predation (for either abundance currency), the Upper Aripo sites are consistently separated from the Lower Aripo sites at extremes of the overall gradient (Figure 2). However, when the intermediate or broad categories are employed this pattern disappears. Reasons for this difference are discussed in the following section.

Predation categorisation

Perhaps the most important finding in this study is that the manner in which predation is quantified determines where a site falls on this predation risk gradient. In other words, the ranking of a given site can shift markedly, depending on which species are considered predators, and the abundance currency being used. When the predator assemblage is expanded to include species that potentially include guppies in their diet, but are less likely to be specialised predators, sites can move from being perceived as very low risk, to having relatively high risk.

In our case, broadening the definition of predation to include two more species, turns the Upper Aripo sites (previously 'no predation' sites) into the two sites ranked as highest in predation risk. This is primarily due to the inclusion of the killifish *A. hartii* in the 'intermediate' category. Although adult *A. hartii* will consume juvenile guppies (Fraser and Lamphere, 2013; Mattingly and Butler, 1994) alongside invertebrates and allochtonous material, they are themselves prey to many of the other predators. Thus, in the absence of larger predators *A. hartii* are typically found at much higher densities (Gilliam *et al*., 1993). Moreover, the size-related nature of the predation risk posed by *A. hartii* differs from that posed by *H. malabaricus* and *C. frenata* both of which are more specialised predators and large enough to capture mature guppies.

Since biological gradients including species richness and predation risk tend to increase from upstream to downstream (Matthews, 1998) we might have expected a correlation between richness and predation risk for one or more of our six categories. However, in no case did we detect a significant correlation between overall species richness and either biomass or numerical abundance across the 16 sites (see SM1). This shows that richness cannot necessarily be used as a surrogate for risk, in this system at least given its spatial scale and the gamma diversity involved (Deacon *et al*., 2017).

The three predation categories used here allow us to gauge the robustness of the gradient to differences in composition. We find some evidence of stability across categories, but note that the rankings of a few sites are dramatically affected. For example, using numerical abundance, the rankings for the broad category are generally consistent with those when the intermediate category is applied (a significant correlation coefficient of 0.96, $p<0.001$), despite six additional species being included. Using biomass, all comparisons of rankings within categories show significant correlations ($p<0.05$).

Although the categories we used in this study were informed by the most up to date information on the ecology of fish in Trinidad's Northern Range, we recognise that other categorisations of predator community may be equally valid. Twenty-one species of fish occur in these sites (Deacon *et al*., 2017). We included the ten species recognised as being, at least occasionally, piscivorous. It is likely that guppies are also predated upon by some of the omnivorous species in the assemblages (Seghers, 1973), but a lack of information on the diet of most species in the system makes justifying which to include difficult. This gap is surprising given how well-studied other aspects of the system are, and further stomach content analysis of all species, supported by stable isotope work, would be an extremely valuable addition to the guppy literature. Expanding our understanding of predator diet and behaviour may allow future studies to 'weight' the contribution of different predators according to their relative risk from a guppy's point of view. We also acknowledge that at some sites predation by decapods (Millar *et al*., 2006) , birds (Seghers, 1974) and even spiders (Deacon *et al*., 2015) contributes to the overall strength of predation pressure, and this should also be taken into account by researchers. A further issue, that we have not addressed here, is that the size distribution of predators, within and amongst species, will also affect risk.

Although ecologists have long debated whether numerical abundance and biomass provide equivalent insights into the way in which species subdivide resources (Pagel *et al*., 1991; Sugihara, 1989; Taper and Marquet, 1996b; White *et al*., 2004) Morlon *et al*. (2009) showed that the shape of the species abundance distribution often changes with abundance currency. In addition, studies at a local scale have found little evidence of a consistent relationship between numerical abundance and biomass (Ehnes *et al*., 2014; Saint-Germain *et al*., 2007; Stead *et al*., 2005; White *et al*., 2007). Our results support these findings and further indicate that site rankings, in terms of predation risk, are not conserved across currency. As such, they add more weight to the conclusion that numerical abundance and biomass cannot be assumed to be surrogates for one another in ecological studies. Investigators thus need to make informed decisions about definitions of predation risk in the context of local knowledge.

Temporal Dynamics

Within most sites, there is considerable temporal variation in both predator numerical abundance and predator biomass, which is what one would expect given natural fluctuations in population size around an average value (Magurran and Henderson, 2010). However, the concordance coefficients indicate that the ranking of sites remained similar over the six years of our study, particularly when numerical abundance was the currency. This suggests that even sampling a site once may be sufficient to position this site appropriately on the predation gradient, meaning that short term studies can still produce meaningful results. It also suggests that other factors, such as climate, may be affecting all sites across the Northern Range similarly, keeping rankings fairly consistent over time.

Biomass produced less temporal consistency in rankings over time than numerical abundance, regardless of the category of predation used (See Figure 5). It is possible that this is because movements of just a few large individuals in or out of a site will have a considerable impact on the total biomass, but only a minor effect on the numerical abundance (Knouft, 2002). Again, the goals of a study will be key in deciding which currency to use. Biomass is thought to be a better indicator

of resource allocation (McGill *et al*., 2007; Thibault *et al*., 2004; Tokeshi, 1993; Török *et al*., 2016) while numerical abundance reflects population dynamics (Brook and Bradshaw, 2006).

Our data represent annual predator abundance for a period of six years. Shorter term variation in predation risk, such as seasonal differences, or longer term changes over evolutionary time, are outside of the scope of this study. Nonetheless, both are worthy of further exploration in relation to the Northern Range system (Brown *et al*., 2006; Carroll *et al*., 2007), especially for those interested in exploring the evolutionary reasons behind the guppy's remarkable flexibility and colonisation success (Deacon and Magurran, 2016), and it would be interesting to further investigate how these different timescales affect the predation risk gradient.

Conclusions and recommendations

Biological gradients tend to be under-utilised in studies of evolutionary ecology, not least in the famous 'natural laboratory' of Trinidad's Northern Range. Here, we have demonstrated that the classic high-risk low-risk dichotomy of fish assemblages in this system represents a spatial gradient, underlain by temporal variation.

Of the approaches compared in this study, using numerical abundance reveals a marginally clearer gradient and more consistent ranking of sites over time, while rankings using a narrow category of predation appear to be more robust to changes in abundance currency. However, before making specific recommendations for the use of one currency or category over another, it will be important to validate these patterns with actual levels of predation risk in these habitats. This is a realistic prospect in this well-studied system and would be a valuable next step. Further, it is important to keep in mind the specific goal of a study when selecting an approach, as different approaches may reveal different features of the system.

Our study suggests that a consideration of predation gradients will lead to a more nuanced understanding of the role of predation risk in behavioural and evolutionary ecology. For example, in the context of Northern Range guppies, better appreciation of temporal change in community structure within sites, as well as of differences in community composition between sites, may help explain the evolution of individual variation in behaviour and decision making. This additional knowledge could also shed new light on the evolution and maintenance of individual variation in male colour patterns. Similar opportunities will exist in other systems. Understanding that predation risk is not just spatially and temporally variable, but also depends on how the predator community is defined in terms of both composition and abundance, will be key here. It also emphasises that the definition of predation risk used in investigations should be be justified and clearly reported in all cases.

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Dominance structure of assemblages is regulated over a period of rapid environmental change

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Abstract

Ecological assemblages are inherently uneven, with numerically dominant species contributing disproportionately to ecosystem services. Marked biodiversity change due to growing pressures on the world's ecosystems is now well documented. However, the hypothesis that dominant species are becoming relatively more abundant has not been tested.

We examined the prediction that the dominance structure of contemporary communities is shifting, using a meta-analysis of 110 assemblage timeseries. Changes in relative and absolute dominance were evaluated with mixed and cyclic-shift permutation models. Our analysis uncovered no evidence of a systematic change in either form of dominance, but established that relative dominance is preserved even when assemblage size (total N) changes. This suggests that dominance structure is regulated alongside richness and assemblage size, and highlights the importance of investigating multiple components of assemblage diversity when evaluating ecosystem responses to environmental drivers.

Keywords: Dominance, timeseries, assemblage, biodiversity

Introduction

The substantial threat to ecosystems posed by the global biodiversity crisis [1] underlines the urgent need to understand how habitats and ecosystems react to change. A number of studies have reported species richness (S) loss, particularly in habitats that have been extensively transformed [2], while other investigations have found no evidence of declining trends [3][4][5]. One explanation for the apparent stasis in species richness in many ecosystems, even in the face of compositional reorganisation, is that assemblages are regulated in terms of their S and total abundance (N). A recent study uncovered evidence for widespread regulation of S and N, where regulation was defined as the assemblage time series returning towards its long term mean following a perturbation [6]. However, the fact that S and N are regulated in many instances does not mean that other attributes of assemblages, such as dominance structure, follow suit. Indeed, we already know that untrending S can be accompanied by marked temporal turnover in species composition [3]. This raises the question of whether or not relative abundance patterns are regulated.

One of the few universal patterns in ecology is that, while most species are rare, a handful of very common species dominate assemblages [7]. These numerically dominant species can contribute disproportionately to ecosystem services, so even a small change in their relative or absolute abundance could have large consequences for ecosystem functioning and sustainability[8]. Dominance patterns may be shifting as a consequence of ongoing environmental changes [9] [10], particularly as dominant species may be generalist species better able to adapt to change [11], but this has not yet been tested.

To explore how dominance patterns are changing in the Anthropocene, we undertake a meta-analysis of change in the numerical abundance of dominant species in consistently monitored assemblages across the globe. We first pose the question: 'are there systematic temporal changes in

dominance?'. Next, we ask if dominance changes as a by-product of shifts in N. If dominance is regulated by the same processes that regulate N, any changes in the abundance (not identity) of the dominant species will be in proportion to change in N. In this scenario, absolute dominance will track changes in assemblage size, but relative dominance will not. On the other hand, a shift in the relative abundance of the dominant taxon (with or without change in absolute dominance) would suggest that assemblages are being restructured as they change in size.

Methods

We used the BioTIME database of monitored local species assemblages[12]. This database contains both animal and plant time series data from around the globe, between 1900 and the present. We selected the 110 assemblages that had at least 10 sample years to avoid artefacts due to short time series duration, and chose only assemblages where abundance had been quantified as numbers of individuals. Of these assemblages, 50 were marine, 49 were terrestrial, and 11 were freshwater.

We applied sample-based rarefaction [3] to each assemblage to account for sampling differences. Analysis was undertaken in R [13]. To focus on long-term trends, we exclude seasonality by summing the abundance of each species each year within each assemblage.

We defined the dominant species as the most numerically abundant taxon in a given year. Note that we are interested only in the abundance of this species, not its identity (which can change between years). Where two species were equally dominant in a year, we selected the first species listed in the dataset. In each year, we computed the following values: assemblage size - the summed abundance of all species in the assemblage (N); absolute abundance of the dominant species - the number of individuals recorded for that species (D_a); relative abundance of the dominant species $D_r=D_a/N$.

To assess whether there was a systematic increase in dominance, we constructed two mixed models using the package lme4 [14] (*Equation S1*). For D_a, $\log_2$ abundance was regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope. Similarly, D_r, the relative dominance of the dominant species each year, was regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope. We then computed the overall rate of change (slope) for both models.

To explore whether observed trends in dominance differ from what would be expected by chance (assuming realistic population dynamics), we next employed a cyclic-shift null model (*sensu* Hallet *et al.* [15], see *Fig. S4*) which preserves within species temporal autocorrelation, but breaks species cross correlations in abundance. To do this we shuffled every assemblage 1000 times using the random shift permutation and calculated its rate of change in both D_a and D_r on each run using the same mixed models as for the observed data above; this gave us a null distribution of 1000 slopes per assemblage. We then asked where the observed slope of dominance change lay relative to the null distribution for that metric and assemblage; observed values below the 2.5% or above the 97.5% quantile were assumed to exhibit a significant shift. We recognise that this analysis does not take account of multiple testing, but note that any correction for this would have the effect of decreasing the number of studies departing from the null expectation.

To examine how D_a and D_r change in relation to assemblage size (*Fig. S5*) we first estimated rates of change of assemblage size using a mixed model of $\log_2$ assemblage size regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope (*Equation S2*). We then used model fitting to assess whether including assemblage size change as a fixed effect that interacts with mean centred year (*Equation S3*) improved model fit in either the absolute or relative dominance models. We also used Pearson's Correlation to assess the relationship between Z scores of the assemblage size model and the two dominance variables, as calculated from the null model results.

Results

We detected no systematic change in either D_a (slope = 0.006, SE = 0.009) or D_r (slope = -0.04, SE = -0.05) (*Fig. 1*). There were no marked differences in rates of change for realms (terrestrial/freshwater/marine) or taxa (Figures S6 & S7). The cyclic-shift null model supported this overall result, but uncovered heterogeneity in the pattern of change. Cases of positive and negative change were slightly less balanced for D_a (decrease in dominance relative to the null expectation: 17 (15%) studies; increase: 33 (33%) studies; no change 60 (54%) studies) than for D_r (decrease: 45 (41%) studies; increase: 33 (30%) studies; no change: 32 (29%) studies (*Fig. S8*).

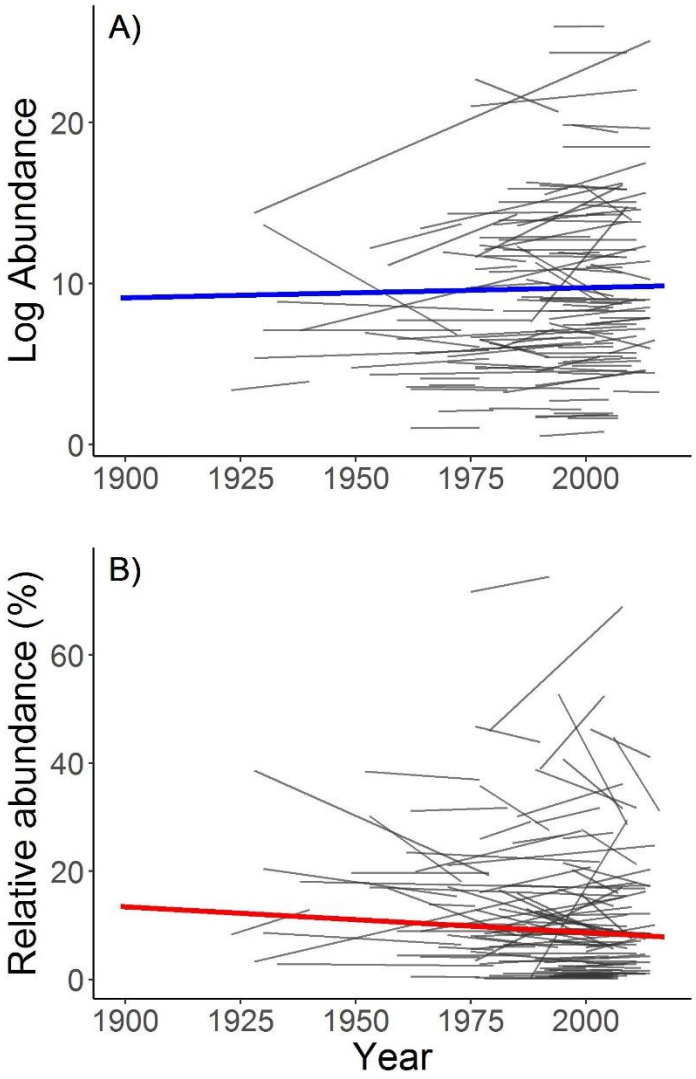

Figure 1. Rates of change of (A) absolute and (B) relative dominance. Each thin grey line represents the trend in dominance within a single assemblage as calculated by the random slopes in the mixed model. The bold lines across both plots show the overall model trend lines.

There was no systematic change in N over time (slope = 0.0069, SE = 0.0070; *Fig. S9*), but this overall trend was also underlain by temporal variation in numerical abundance within and among assemblages. D_r on average represents less than 20% of N in the majority (86) of assemblages (*Fig. S10*). At the assemblage level, Z scores of changes in D_a were correlated with Z scores of changes in total N (r = 0.67; *Fig. 2a*). Including rate of change in N, and its interaction with time, improved the fit of the D_a model (p = < 0.001), supporting a positive relationship between change in absolute dominance and change in assemblage size.

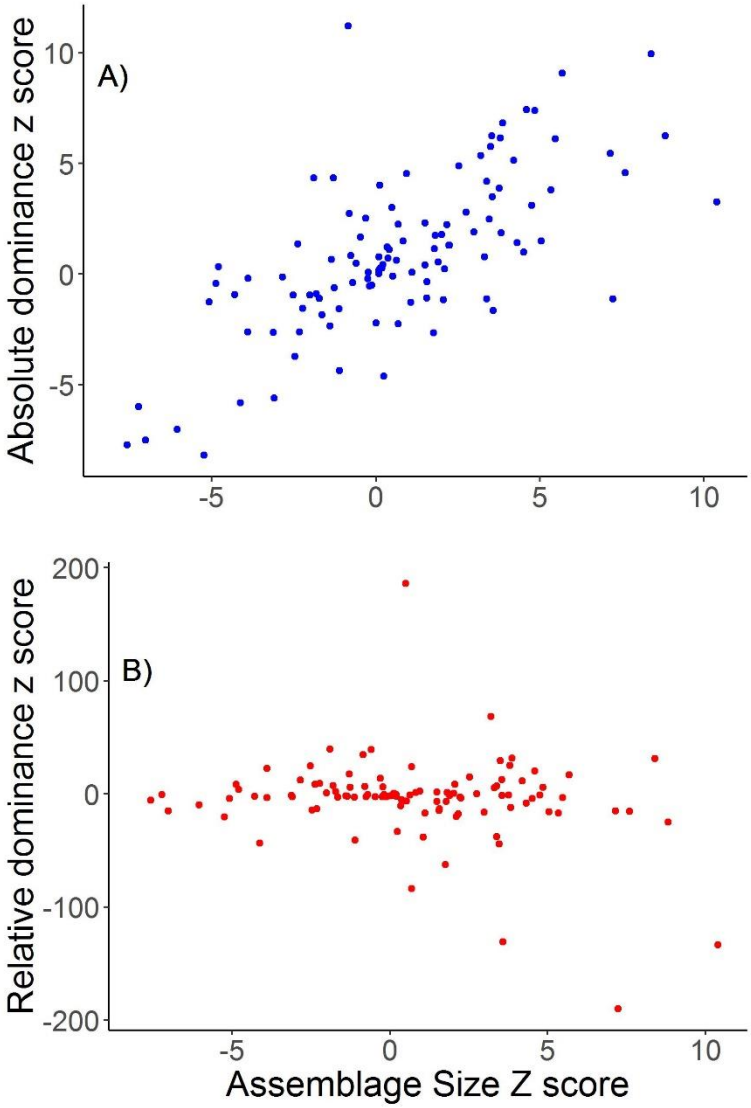

Figure 2. Z scores from the assemblage size change model against both the absolute (A) and relative (B) dominance change models. A positive relationship is evident for absolute dominance but not relative dominance.

There was, conversely, no relationship between Z scores of changes in N and changes in D_r (r = -0.21; *Fig. 2b*). Including rate of change of N in the D_r change model did not improve model fit (p = 0.3).

Discussion

Although dominance and species richness components of assemblages contain orthogonal information on biodiversity [16] there has, until now, been only limited understanding of how dominance structure changes through time. Despite predictions of widespread assemblage restructuring [16] we found no evidence of a systematic increase in dominance. However, shifts in dominance were present and generally tracked changes in overall assemblage size. In other words, dominant species continued to account for roughly the same fraction of the assemblage even when it contracted or expanded in size. As a result, there is little support for the idea that common species are increasingly dominating ecosystems.

Many different external drivers, such as climate change [17], pollution [18] and land use intensity [10], have the potential to alter the patterns of dominance. Nonetheless, our analyses show that in the assemblages we studied, dominance structure is not undergoing any directional change. This

suggests that dominance is being regulated alongside S and N [6]. The potential mechanisms underlying this phenomenon are numerous, and include niche and fitness differences (see HilleRisLambers *et al*. [19] for further discussion).

The abundance and identity of a species combine to shape its influence on ecosystem functioning [20]. Indeed, the identity of the dominant species is the main driver in influencing biomass production, community composition and functioning [21]. As such, there could be shifts in ecosystem functioning despite no change in dominance structure. Elucidating these shifts is a key challenge in building a predictive framework of biodiversity change in a rapidly changing world [22].

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